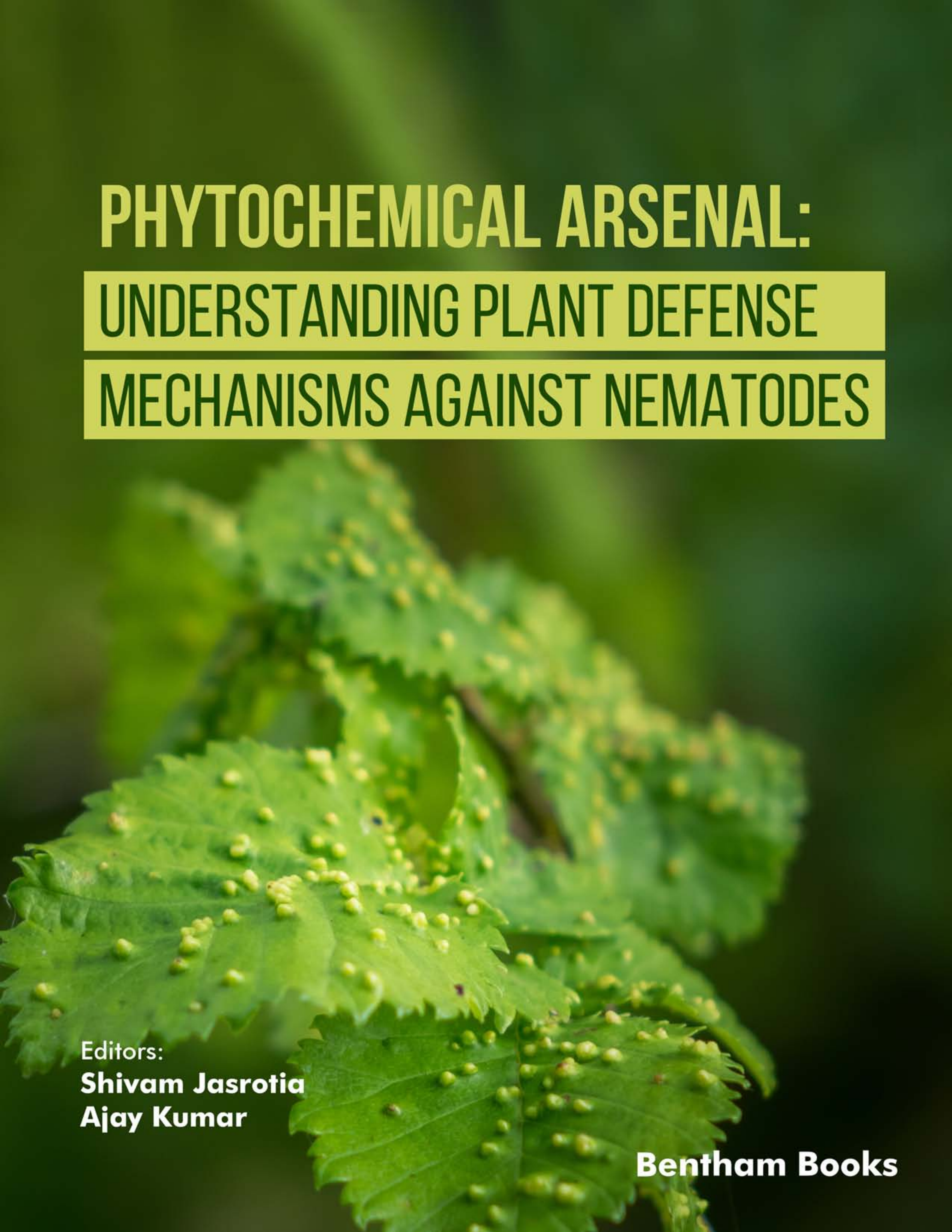

PHYTOCHEMICAL ARSENAL: UNDERSTANDING PLANT DEFENSE MECHANISMS AGAINST NEMATODES

Editors:
Shivam Jasrotia
Ajay Kumar

Bentham Books

Phytochemical Arsenal: Understanding Plant Defense Mechanisms Against Nematodes

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FOREWORD

In recent years, the field of plant-nematode interactions has gained increasing attention due to the significant economic losses caused by nematode infestations in agricultural crops. As researchers and professionals seek effective and sustainable strategies to manage nematode pests, understanding the intricate defense mechanisms employed by plants becomes paramount. The book "Phytochemical Arsenal: Unveiling Plant Defense Mechanisms Against Nematodes" offers a comprehensive exploration of the fascinating world of plant-nematode interactions and the role of phytochemicals in plant defense.

The unique aspect of this book lies in its focus on the diverse array of phytochemicals produced by plants as their defense arsenal against nematodes. By examining the biosynthesis, mode of action, and ecological significance of these phytochemicals, the authors shed light on the complex interactions between plants and nematodes. The book delves into the mechanisms through which phytochemicals deter, repel, or inhibit nematodes, providing valuable insights into the multifaceted strategies that plants have developed to defend themselves.

With contributions from experts in the fields of plant biology, biochemistry, molecular biology, and agricultural sciences, this book presents a comprehensive and interdisciplinary approach to understanding plant-nematode interactions. It consolidates the latest research findings and scientific advancements, offering a valuable resource for researchers, academicians, and professionals involved in plant pathology, agronomy, crop science, and pest management.

The book goes beyond theoretical discussions by exploring the potential applications of plant-derived phytochemicals in developing sustainable nematode management strategies. It delves into topics such as biopesticides, breeding programs, and biotechnological interventions, providing practical insights into how phytochemicals can be utilized to combat nematode infestations effectively.

As a result of its in-depth exploration of the subject matter, this book serves as an essential guide for researchers and practitioners seeking to enhance their understanding of plant-nematode interactions and develop innovative approaches to nematode management. Its comprehensive coverage, combined with the author's expertise and the integration of case studies and success stories, makes it a valuable resource for both academia and industry.

I commend the authors for their dedication and the wealth of knowledge they have brought together in "Phytochemical Arsenal: Unveiling Plant Defense Mechanisms Against Nematodes." I am confident that this book will be a valuable addition to the scientific literature on plant-nematode interactions and will inspire further research and innovation in the field. It is my pleasure to endorse this book and recommend it to all those interested in advancing our understanding and management of nematode pests in agriculture.

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PREFACE

In the realm of agriculture, nematodes have long been recognized as formidable adversaries, capable of wreaking havoc on crops and causing significant yield losses worldwide. As the need for sustainable and eco-friendly solutions to combat nematode infestations becomes increasingly urgent, exploring the defense mechanisms employed by plants takes center stage. This book, “Phytochemical Arsenal: Unveiling Plant Defense Mechanisms Against Nematodes,” delves into the fascinating world of plant-nematode interactions, with a particular focus on the crucial role of phytochemicals in plant defense.

The journey into the intricate realm of plant-nematode interactions begins with an exploration of the different types of nematodes, their life cycles, and the damage they inflict upon agricultural crops. This foundation sets the stage for understanding the challenges that plant populations face and the importance of unraveling their defense mechanisms against these microscopic parasites.

The book then delves into the diverse and captivating world of phytochemicals, nature's own arsenal of defense compounds produced by plants. Through detailed discussions, readers will gain insights into the various classes of phytochemicals, their biosynthesis pathways, and their roles in defending plants against nematode infestations. From alkaloids and terpenoids to phenolic compounds and glycosides, the book uncovers the intricate chemistry behind these compounds and their impacts on nematode behavior and physiology.

Understanding the mode of action by which phytochemicals combat nematodes is vital in unraveling the intricacies of plant defense mechanisms. This book explores the fascinating interactions between phytochemicals and nematodes, shedding light on how these compounds disrupt nematode feeding, reproduction, behavior, and mobility. Through this exploration, readers will gain a deeper understanding of the remarkable strategies plants have evolved to fend off nematode attacks.

Moreover, the book addresses the influence of environmental factors on the production and efficacy of phytochemicals. It delves into the impact of abiotic and biotic factors on phytochemical synthesis, providing insights into how environmental conditions can be manipulated to enhance plant defense against nematodes.

As researchers and practitioners seek practical applications for their knowledge, the book delves into the exploitation of phytochemicals for nematode management. It examines the potential of phytochemical-based biopesticides, breeding strategies for developing nematode-resistant plants, and biotechnological interventions that harness the power of genetic engineering and beyond. By examining these strategies, the book offers valuable guidance on how to utilize phytochemicals in integrated pest management programs, ultimately contributing to sustainable and effective nematode control.

Throughout the book, case studies and success stories highlight real-world applications and demonstrate the practical implications of phytochemical-based nematode management strategies. These cases provide valuable insights into the challenges faced, lessons learned, and potential pathways for future research and innovation.

In conclusion, “Phytochemical Arsenal: Unveiling Plant Defense Mechanisms Against Nematodes” aims to provide a comprehensive and insightful exploration of the fascinating world of plant-nematode interactions. It consolidates the latest research findings, scientific advancements, and practical applications, making it a valuable resource for researchers, academicians, and professionals in the fields of plant pathology, agronomy, crop science, and pest management.

We hope that this book will serve as an informative and thought-provoking guide, inspiring further research, collaboration, and innovation in the realm of nematode management. We extend our gratitude to all the contributors who have shared their expertise and knowledge, making this book possible. Our sincere hope is that it will contribute to the development of sustainable and effective strategies to protect our crops from the perils of nematodes.

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CHAPTER 1

Overview of Plant-Nematode Interactions and Understanding Plant Defense Mechanisms

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Abstract: Plant-nematode interactions represent a dynamic interplay between parasitic nematodes and their host plants, influencing plant health and agricultural productivity worldwide. This chapter provides a comprehensive overview of the mechanisms underlying plant defense against nematode infestation. It begins with an exploration of nematode parasitism strategies, including sedentary endoparasites and migratory ectoparasites, the discussion delves into the molecular and biochemical mechanisms employed by plants to recognize nematode invasion and mount defense responses. Key topics include the role of plant hormones such as jasmonic acid and salicylic acid in signaling pathways, the activation of defense-related genes, and the induction of physical barriers to nematode penetration. Furthermore, recent advances in understanding plant-nematode interactions, such as the discovery of nematode effectors and their manipulation of plant immunity, are highlighted. Additionally, the chapter examines the potential application of biotechnological approaches, such as breeding for nematode resistance and the use of biocontrol agents, in managing nematode infestations sustainably. By elucidating the intricate mechanisms of plant defense against nematodes, this chapter aims to contribute to the development of effective strategies for enhancing crop resilience and ensuring global food security. By synthesizing current knowledge and research findings, this chapter contributes to a comprehensive understanding of plant-nematode interactions and provides insights into novel avenues for enhancing plant resistance to nematode pests. Ultimately, elucidating the intricacies of plant defense mechanisms against nematodes holds promise for sustainable agriculture practices and the development of resilient crop varieties in the face of evolving pest pressures.

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Keywords: Plant immunity, Nematode effectors, Plant-nematode interactions, Plant defense mechanisms, Molecular signaling pathways.

INTRODUCTION TO PLANT-NEMATODE INTERACTIONS

Plant-parasitic nematodes (PPNs) are small microscopic creatures that pose significant threats to agriculture and horticulture by feeding on the roots of plants, leading to decreased crop productivity, hindered growth, and occasionally plant demise. They represent a great problem in global crop production as they bring about substantial economic losses every year [1 - 4]. Among these, inactive endoparasitic nematodes under the family Heteroderidae, such as root-knot nematodes (RKNs) (*Meloidogyne* spp.) and cyst-forming nematodes (CNs) (*Heterodera* and *Globodera* spp.), are particularly troublesome [3, 5].

CNs typically have a limited range of hosts, while RKNs are known for their ability to parasitize a wide variety of flora on this planet [6]. Among CNs, the most harmful species are primarily those belonging to the *Heterodera* and *Globodera* genera [7]. Four prevalent and adaptable RKN species are *Meloidogyne incognita*, *M. javanica*, *M. arenaria* (apomictic), and *M. hapla* (automictic), which cause substantial agricultural damage. Both CNs and RKNs remain within the plant roots for a major part of their life cycle, typically completing their reproductive cycle within 2-3 fortnights [8]. They possess specialized structures allowing efficient penetration of plant tissues, modification of root cells, and extraction of nutrients for their growth and reproduction. These nematodes employ complex mechanisms to parasitize host plants, leading to the formation of specific nourishing sites—giant cells for RKNs and syncytia for CNs—within plant roots. Giant cells arise from the transformation of approximately six vascular root cells, undergoing repeated division of their nuclei not followed by cell division, resulting in enlarged cells with multiple nuclei that can be more than 300 times larger than typical cells. Surrounded by dividing cells, these enlarged cells lead to the creation of characteristic galls [9 - 11]. The formation of a syncytium begins when the root cell wall partially dissolves and the protoplasts of the first infected vascular cell merge with adjacent cells. This process can lead to the formation of syncytia that include more than 200 cells. Syncytia, like giant cells, share several traits such as an expanded endoplasmic reticulum, broken down vacuoles, rearranged cytoskeletons, reinforced cell walls with localized protrusions, extensive mitochondrial networks, and nuclei that have undergone endoreduplication [10, 12]. These specialized nematode feeding sites (NFS) are crucial as they supply nutrients to the nematodes during the non-mobile stages of their life cycle.

Female RKNs deposit their eggs encased in a gel-like substance on plant roots, whereas CNs embed their eggs within the hardened body of the dead female, forming a cyst. These parasites induce several changes in the morphology, biochemistry, and molecular structure of plant root cells to create nourishing sites. This alteration is primarily driven by substances the nematodes emit through their stylets, which trigger a series of signaling events within the host cells [10, 12]. The interaction between the nematodes and the plants begins when the second-stage juvenile nematodes (J2) move towards the roots, attracted by substances the roots emit [13]. In the absence of defensive reactions from the plant, such as the production of reactive oxygen species (ROS) and the deposition of callose, the nematodes penetrate the root cells and target the vascular system to establish their NFS [13]. These sites then serve as the main nutritional sources for the nematodes as they continue their development. Nematodes secrete specific molecules, referred to as "effectors," that help them invade the host roots, evade plant defenses, and modify the root cells to create specialized NFS [13]. These effectors are primarily produced in the nematodes' three esophageal salivary glands and delivered into plant cells *via* the stylet, which functions like a syringe. The activity of these glands changes over time; initially, the two subventral glands (SvG) are primarily active in aiding J2 penetration and movement within the root, but as the nematode matures, secretion mainly occurs from these glands and particularly the dorsal gland (DG) [13, 14]. Additionally, effectors can also come from other secretory structures like the chemosensory amphids or be directly secreted through the nematode's cuticle. Research has mainly focused on the protein-based effectors [15 - 19], though there are indications that other molecules such as phytohormones also significantly impact these interactions [20].

Nematode secretions are essential for initiating the formation of NFSs, containing a variety of components such as CWDEs, Avr proteins, and transcription factors [21, 14]. Through these effector proteins, PPNs interact with host genes and proteins, facilitating successful parasitism [21 - 23]. These secretions induce significant changes in host gene regulation *via* the stylet, prompting the conversion of parasitized root cells into specialized NFS [24]. Moreover, nematode effectors can manipulate plant metabolic and developmental pathways to induce NFS formation and suppress host defense mechanisms [21, 23]. The initiation of NFSs begins with J2s hatching from eggs and migrating towards roots. They initiate infection by penetrating the epidermal cells of the root, using their stylet to create openings in the cell wall (Fig. **1**). These nematodes then navigate through the root's cortical cells toward the vascular cylinder. The choice of ISC varies by species; for instance, *Globodera* species often target cells in the inner cortex or endodermis [25, 26], whereas *H. schachtii* commonly selects cells in the cambium or procambium of the vascular cylinder [27]. Using their stylet, J2s breach the ISC's cell wall and inject esophageal gland secretions into the

CHAPTER 2

Evaluation of Damage and Protection in Nematode Infected Plants

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Abstract: Nematodes, especially plant-parasitic ones, do a great deal of harm to plants, mostly by attacking the root systems. These tiny roundworms persist in the topmost layer of soil and eat the belowground portion, which prevents the plant from getting the vital nutrients and water it needs. As a result, afflicted plants show signs such as stunted development, which is noticeable even under ideal circumstances, and withering even in the presence of adequate soil moisture. The damage also affects the leaves, which frequently become yellow as a result of nutritional shortages brought on by compromised root function. Reduced yields are frequently the result of damaged root systems that are unable to sustain strong plant development. Additionally, the induction of lesions, galls, and deformities on roots caused by nematode feeding exacerbates the suffering experienced by plants and creates openings for other infections. In severe cases-especially in young or weak specimens - the cumulative effects result in plant death. These consequences highlight the serious threat that nematodes represent to agricultural output, which calls for the application of a number of management techniques to lessen their negative effects and protect crop yields and health. In order to combat nematode infestations, plants have developed a variety of defense systems that include both chemical and physical tactics. To combat nematode infection, plants have developed several defense mechanisms which include both physical and chemical nature. Physical barriers that prevent nematodes from penetrating roots and causing harm include thicker cell walls, lignification, and the creation of suberin layers. In reaction to nematode infestation, plants simultaneously release an abundance of secondary metabolites. These substances, which have nematicidal qualities and directly target nematodes or prevent them from establishing

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feeding sites, include phytoalexins, phenolics, and terpenoids. Keeping the above mentioned facts in mind, this chapter tends to focus primarily on the damages caused by the plants to their hosts and the nature of defense strategies adopted by them.

Keywords: Allelochemicals, Chlorosis, Defense, Host, Nematodes, Oxidative damage.

INTRODUCTION

With global distribution, root-knot nematodes (RKN) are among the destructive families of plant parasitic nematodes (PPNs) [1]. Among more than 100 species in the genus *Meloidogyne*, "major" species include *M. arenaria, M. incognita, M. hapla*, and *M. javanica* [2]. Due to worries about environmental safety and human health, biological control agents (BCA) are receiving more attention as they appear to represent the future of affordable, environmentally friendly, and sustainable agriculture [3]. These nematodes are often disregarded since most farmers are ignorant of their presence and the symptoms they cause. More than 90% of the anticipated losses are thought to have been caused by the most prevalent species, which impact both field and vegetable crops: *M. arenaria, M. hapla, M. javanica,* and *M. incognita* [4]. The most pervasive and destructive plant parasites are RKN (*Meloidogyne* spp.), which can reduce yield output by 20-50% across large areas of farmed land [5, 6].

In India, these nematodes cause output losses of 16.67, 14.10, 27.21, and 12.3% in tomato, banana, brinjal, and okra, respectively. These worms' attacks worsen the harm by providing a pathway for additional pathogens to infect the host. The deadly, tiny root-knot nematodes cost agriculture $85 billion annually worldwide. In India, it is projected that nematodes cause agricultural losses worth Rs 242.1 billion annually. Worldwide, nematodes still pose a threat to agricultural crops [7]. Up to a 23% decrease in hot pepper production nationwide has been ascribed to RKNs [8]. Merely 10% of all recognized nematode species are harmful to plants, meaning they feed on plants, which hinders crop growth and production efficiency. In tropical and subtropical regions, PPNs have been predicted to bring about a 14.6% reduction in agricultural output, whereas in industrialized regions, the loss is 8.8%. According to study [9], PPNs cause around 10% of the global crop output losses that occur each year or $173 billion in US dollars. The availability of food is significantly impacted by PPNs because of the sharp growth in food demand brought on by the expected 35% growth in the number of humans by 2050. According to some estimates, dietary trends and constant increases in the population would lead to a 75% increase in food consumption between 2010 and 2050 [10]. Studies show that tomato production is decreased by RKN by 26.5% to 73.3%, costing the global tomato industry around $125 billion annually in losses

[11]. Generally speaking, foliar indications of nematode infection include nitrogen deficiencies and tomato production losses due to root-knot nematodes.

According to a study [12], RKN rank the top among the 10 most significant genera of PPNs as well as first among the five primary plant illnesses. They are widely distributed geographically, have a wider host range, and have a potent damaging ability. They have been connected to a number of plant illnesses that aggravate wilt diseases and create disease complexes [13].

NEMATODE PATHOGENESIS IN PLANTS

The phylum Nematoda contains nematodes, which are tiny creatures that may be found in a range of environments such as freshwater, aquatic, soil, and marine. They can be free-living organisms or parasites on bacteria, fungi, plants, or mammals. Due to their widespread occurrence in nature, they pose a threat to humans, animals, and plants. They also cause losses in agricultural productivity on a worldwide scale [14, 15]. Their eating habits and surroundings are the main factors used to categorize them. In contrast to ectoparasites, which feed through stylets inside root cells, endoparasites invade roots. Sedentary parasites, RKNs grow knot-like forms on root surfaces and develop specialized organs to get nutrients from their hosts [16]. In addition, they cause damage to the plants by decreasing water absorption and mineral availability due to disturbances in root architecture. Additionally, they increase the host plants' susceptibility to disease attacks [17].

At the elongation zone, the juveniles in their second stage (J2) penetrate the plant roots and break down the cell wall using enzymes that degrade cell walls, like glucanases, pectinases, and chitinases [18]. They go into the vascular zone from the apoplast region, where they settle in and create large numbers of feeding cells. These enormous cells are assumed to be the precursors of hyperplasic tissues and gall formation. In response to nematode effectors, plants disrupt the molecular pathways that link them [19]. Repetitive mitosis, cytokinesis, and duplication are partially completed by the large cells, leading to incomplete division or mitosis and the amplification of DNA necessary for giant cell proliferation [20]. Galls arise once asynchronous development is complete, and this is intimately linked to the infectious stage of RKN [21]. Additionally, giant cells form in the vicinity of cell wall zones, producing asymmetric membrane thickenings that facilitate solute transport and cell invasions (Fig. **1**).

Stunted Growth

Nematodes damage the root system, hindering the capacity of plants to take up water and nutrients from the soil, which causes stunted growth and poor overall

CHAPTER 3

Arsenal Role of Phytochemicals in the Defense System of Plants and the Modulation of Biosynthesis of Phytochemicals

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Abstract: Plants are present ubiquitously on Earth as faunal diversity. Both interact with each other at one or another stage. This interaction can be positive or negative for plants. Interaction for the purpose of pollination is classified as positive interaction whereas faunal diversity (mostly arthropods) is attacking plants to fulfill their food requirement. To defend themselves against this attack by herbivorous animals, plants synthesize some bioactive compounds. Plants release these compounds either to kill or repel these herbivorous animals. Hence it is a direct approach to counter these attacking animals. An indirect approach is also used by some plants where plants produce nectar to attract ants. These ants feed on this nutritious nectar and defend the plants from herbivorous insects that eat the plant's leaves. Compounds synthesized by plants can have noxious odors, and excessive stimulation and some compounds become toxic after ingestion. Ingestion of these compounds can cause many problems such as vomiting, nausea hallucinations convulsions, and even death of the organism.

Keywords: Alkaloid compounds, Plant defense system, Phytochemicals, Phenolics, Terpenoids.

INTRODUCTION

Plants develop complex defense mechanisms against biotic and abiotic stressors when sufficiently opposing forces arise from natural systems. Every living plant cell has the capacity to recognize incoming pathogens and mount an inducible defense against them, which can include the release of poisonous compounds, enzymes that break down infections, and intentional cell death. The production and maintenance of defense-related proteins and poisonous chemicals demand significant energy costs and food requirements, plants frequently wait until infections are discovered before creating these compounds [1]. A large array of

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defense mechanisms to fend off disease attacks from fungi, bacteria, and viruses as well as physical, chemical, and biological stressors include cold, drought, heavy metals, and pollution. The release of secondary metabolites like phytoalexins, tannins, and polyphenolic compounds, and the generation of pathogenesis-related (PR) proteins provide this resistance [2]. Around 17 families of such defense related characteristics, such as antibacterial, antifungal, antiviral, anti-oxidative activity, and chitinase and proteinase inhibitory activities, have been found and isolated [3 - 6].

PLANT DEFENSE SYSTEM

A wide range of adversaries, such as infections and herbivores, frequently attack plants. Plants produce phytochemicals as a means of signaling molecules that can deter herbivores and guard against diseases [7, 8]. These phytochemicals are estimated to be more than 2,00,000 low molecular weight which are evolved in response to ecological stressors, namely biotic stressors like herbivore attacks [9, 10]. Most of the plants are reported to produce a variety of phytochemicals, including flavonoids, phenolics, alkaloids, and essential oils [7, 11]. All these substances have the ability to tackle herbivore attacks; some can kill insects instantly upon incorporation, while others can delay or disrupt the development of herbivores, reduce digestive efficiency, thereby lowering resistance to disease and limiting fecundity, repel herbivores, or draw in organisms from a different trophic level [10, 12]. These categories include a number of molecules that protect plants as discussed ahead in Fig. (**1**).

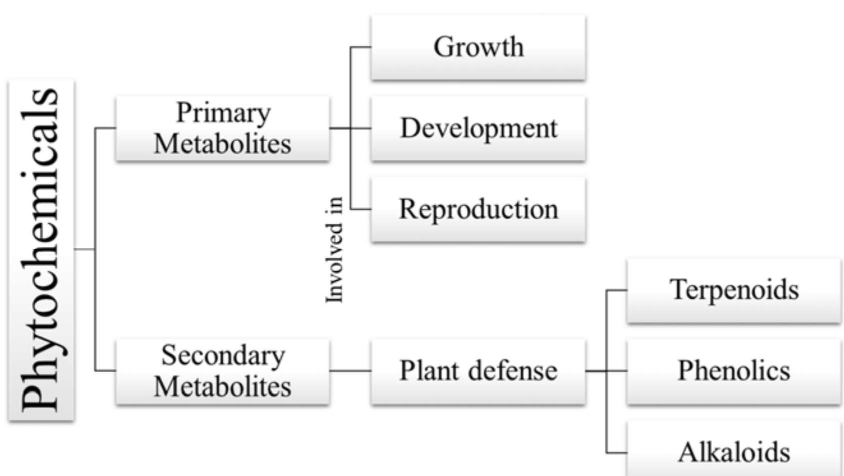


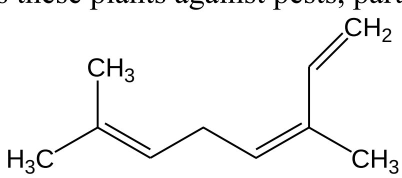
Fig. (1). Functions classification of phytochemicals.

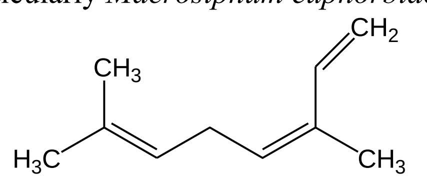
- Isoprene-derived terpenoids including steroids and saponins,
- N-containing alkaloids; (poly)phenolic compounds including flavonoids, tannins; glucosinolates; cyanogenic glucosides,
- Amino acid derivatives such as γ-amino butyric acid (GABA),
- But also peptides/ proteins (proteinase inhibitors, lectins, sporamin); latex; and
- Inorganic compounds (SiO_2, oxalate, selenium) are efficient defensive substances [10, 12].

Terpenoids

Terpenoids play a vital role in inducing chemical deterrents to herbivores. In many plant-pathogen interactions, one of the defense mechanisms against an attack is the synthesis of terpenes, which function as specific or broad pathogen inhibitors. The role that terpenes and terpenoids play in resistance to plant diseases, including bacteria, viruses, and fungi, as well as, when applicable, their vectors are also inhibited [13]. With over 22,000 chemicals reported, terpenoids, or terpenes, are the biggest class of secondary metabolites found in all plants. The most basic terpenoid is the hydrocarbon isoprene (C_5H_8), a volatile gas that is released in enormous quantities during photosynthesis and which may shield cell membranes from harm brought on by intense light or heat. The quantity of isoprene units utilised to create terpenoids determines their classification. Sesquiterpenoids (three units), diterpenoids (four units), and triterpenoids (six units) are among the constituents of monoterpenoids, for instance.

β-ocimene: Ocimenes (3,7-Dimethylocta-1,3,6-triene) are a group of isomeric hydrocarbons. The ocimenes are monoterpenes found within a variety of plants and fruits. The ocimenes are often found naturally as mixtures of the various forms. The mixture, as well as the pure compounds, are oils with a pleasant odor. They are used in perfumery for their sweet herbal scent and are believed to act as plant defense and have anti-fungal properties. In tomatoes and tobacco, β-ocimene defends these plants against pests, particularly *Macrosiphum euphorbiae* [14].





cis-β-Ocimene *trans*-β-Ocimene

Terpinolene: Terpinolene (3,7-Dimethylocta-1,3,6-triene) is a natural product thathas been isolated from a variety of plant sources like *Camellia sinensis, Hypericum foliosum, Melaleuca alternifolia, etc.* Terpinolene is a p-menthadiene with double bonds at positions 1 and 4 [8]. It has a role as a sedative, an insect repellent, a plant metabolite, and a volatile oil component. They are all colorless

CHAPTER 4

Phytochemicals' Classes Involved in Nematode Defense and their Related Activities

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Abstract: Plant parasitic nematodes (PPNs) are one of the most lethal pests that have emerged in the past years. These nematodes are microscopic in size, cylindrical in shape, and inhabit mostly terrestrial ecosystems. They account for a significant biotic limiting factor that hampers crop yield and productivity. PPNs are majorly categorized into three categories such as lesion nematodes (*Pratylenchus* spp.), Root-knot nematodes (*Meloidogyne* spp.), and cyst nematodes (*Heterodera* and *Globodera* spp.). They are known to be the primary cause of pest infestation among other PPNs. Terpenes, flavonoids, alcoholics, and phenolics are essential plant secondary metabolites with a reliable potential to control the PPN population. Reports have shown that they reduce the gall size, inhibit egg hatching, increase the mortality rate of infective juveniles (IJs), *etc*., which lead to the death of IJs and hence protect the crops against PPNs. Such studies elucidate the importance of using plant phytoconstituents as a natural alternative to hazardous chemical pesticides, which are dangerous to humankind and nature. This chapter culminates the efficiency of plant secondary metabolites and their significance in killing root-knot nematodes majorly of different species infesting commercial agricultural crops at different life cycle stages.

Keywords: Egg hatching, Infective juvenile, Plant parasitic nematodes, Root knot nematode, Secondary metabolites.

INTRODUCTION

Agriculture contributes significantly (4.3%) to the world's Gross Domestic Product (GDP). Plant Parasitic Nematodes (PPNs) are profoundly known to cause severe damage to most of the agriculturally important plants in high demand and

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consumed by people worldwide. Their attack is responsible for 21.3% of crop loss, which is equivalent to nearly 1.58 billion USD yearly, in which 19 horticultural crops were assessed at a loss of 50,224.98 million and 11 field crop losses of 51,814.81 million. Among PPNs, the *Meloidogyne graminicola*, a root-knot nematode for rice, is responsible for a loss in the crop yield of 23,272.32 million [1]. Fruit crops such as citrus and banana suffered losses of 9828.22 and 9710.46 million; other vegetable crops such as tomato and okra bear losses of 6035.2 and 2480.86 million [1]. In recent years, researchers have developed many strategies to combat the action of PPNs to alleviate the burden of loss of the agricultural economy. Plant secondary metabolites have shown remarkable and promising results lately against different species of plant parasitic nematodes at different stages of the nematode life cycle. Herein, we have discussed the plant secondary metabolites belonging to different classes and their action against the plant parasitic nematodes.

PLANT SECONDARY METABOLITES

The medicinal plants show diverse pharmacological activities due to the phytochemical constituents present in them. Based on their involvement in the metabolic processes, they are broadly categorized into primary and secondary metabolites. Primary ones play an important role in the basic metabolic and physiological functioning of life and are found similar in most living cells. The secondary metabolites play a vital role in alleviating many ailments in traditional medicine systems and folk uses. Plant metabolites prove to be a boon in the field of drug discovery in modern medical systems. Secondary plant metabolites are classified according to their chemical structures into various classes such as terpenes, phenolics, alkaloids, flavonoids, glucosinolates, *etc.* [2].

The secondary metabolites show different biological effects that provide a scientific basis for the utility of herbs in many traditional practices used by ancient communities across the globe. They have shown antifungal, antiviral, and antibiotic properties and thus protect the plants from lethal pathogens. The list of phytoconstituents and their action have been provided in Table **1** and chemical structure and target action are presented in Figs. (**1** and **2**).

Table 1. List of phytochemical constituents and their nematicidal activity against different stages and species of plant parasitic nematodes.

Secondary Metabolite Source	Secondary Metabolites and the Class of Phytoconstituent	Mode of Action	Crop	Target Nematode	Inference	References
Artemisia elegantissimia A. incisa	Isoscopletin (Coumarin), Carbofuran and Apigenin (Flavonoid)	Mortality of J2s and egg hatch inhibition	Tomato	*Meloidogyne incognita*	Inhibition with (90.0%) and (96.0%) at 0.3 mg/mL concentration.	[27]

(Table 1) cont.....

Secondary Metabolite Source	Secondary Metabolites and the Class of Phytoconstituent	Mode of Action	Crop	Target Nematode	Inference	References
Carvone, cuminaldhyde, linalool, and cineole	J2 hatching inhibition and mortality.	Inhibition of egg hatching	Tomato	*Meloidogyne incognita*	LC_{50} values: 123.5, 172.2, 354.9, 466.4, & 952.3 µg/mL, respectively.	[31]
Aristolochia mollissima	Aristolochic acid I, aristololactam I, aristololactam W	J2 Mortality	-	*Meloidogyne javanica*	LC_{50} values of 45.25, 36.56, 119.46 mg· L^{-1} after 96 h.	[32]
Syzygium aromaticum	*para* methyl benzoic acid, 3-*O*-*trans*-*para*-coumaroylmaslinic acid, methyl maslinate, maslinic acid	-	-	*Meloidogyne incognita*	Mortality inhibition (88–92%	[33]
Lavandula intermedia (Other species: *abrialis*, *cerioni*, *sumiens)*	Linalool (Terpene)	Inhibition of egg hatching along with J2 mortality; reduction of galls, eggs	Tomato	*Meloidogyne incognita*	EO; 24.9 µg/mL−1, 1.2 µg/mL−1, 17.4 µg/mL−1	[34]
Lavandula intermedia (Other species: *abrialis*, *Cerioni*, *sumiens)*	Linalool (Terpene)	Inhibition of egg hatching along with J2 mortality	-	*Pratylenchus vulnus*	Mortality Rate 65.5%, 67.7%, and 75.7% (4 h of exposure)	[34]
Monarda didyma, *Monarda fistulosa*	γ-terpinene (Terpenoid), o-cymene(Aromatic Hydrocarbon), Carvacrol(Monoterpenoid)	J2 mortality, egg-hatching inhibition, galls and eggs reduction in soil	Tomato	*Meloidogyne incognita*	(J2 mortality)1.0 µL mL−1; 12.5 µL mL−1 (24 h) (egg hatching)500 &1000 µg mL−1 (24-48 h)	[35]
Mentha longifolia	piperitone oxide (Monoterpene)	Inhibition of J2 mortality and egg hatching inhibition	-	*Meloidogyne graminicola*	EO; 15.62-1000 ppm (96 h)	[36]
Mentha spicata L.	Carvone (Monoterpene), limonene(Cyclic Monoterpene)	J2 mortality, reduction of galls and eggs	Coleus	*Meloidogyne javanica*	EO; 1000, 2000, 3000, 4000, & 5000 ppm (v/v) for 24 h; 48 h; 72 h	[37]
Thymus vulgaris L.	Thymol, ρ-cymene	J2 mortality, Reduction of the galls and eggs	Coleus	*Meloidogyne javanica*	EO; 1000, 2000, 3000, 4000,& 5000 ppm (v/v) (24 h; 48 h;72 h)	[37]
Mentha spicata L.	-	-	Pepper	*Meloidogyne incognita*	EO; 5% (v/v) (72 h)	[38]
Basilicum L.	SabineneMonoterpene), Myrcene(Monoterpene) Transcaryophyllene (Sesquiterpene)	J2 mortality, reduction of galls	Pepper	*Meloidogyne incognita*	EO; 5% (v/v) (72 h)	[38]

CHAPTER 5

Mode of Action of Phytochemicals During Physiological and Biochemical Interactions with Nematodes

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Abstract: The proliferation of plant-parasitic nematodes as formidable agricultural pests poses a significant global threat to crop productivity. Despite their diminutive size, these organisms inflict substantial economic losses, with global damage surpassing that caused by insect pests. The cryptic nature of nematode infections renders them particularly insidious, often leading to underestimation and inadequate management. Beyond their intrinsic harmful effects, plant-parasitic nematodes exacerbate crop damage by forming synergistic disease complexes with other pathogenic microorganisms. Nematodes utilize diverse strategies to breach plant host tissues, with a particular emphasis on the root-knot and cyst-forming nematodes—two prominent groups that inflict severe agricultural damage. The evolution of plant defense mechanisms is an intrinsic biological response by which plants counteract nematode parasitism. Plants deploy receptor molecules against nematode effectors, facilitating resistance by either preventing nematode penetration or by producing nematicidal proteins that mitigate nematode pathogenicity. The activation of plant defense-related genes and the synthesis of defensive hormones are pivotal in enhancing plant resilience against nematode invasion. However, under certain conditions, these defensive strategies may inadvertently augment nematode parasitism. Common symptoms indicative of nematode infestation include tissue necrosis, gall formation, cyst development, and stunted plant growth. This chapter delves into the current understanding of plant-nematode interactions, emphasizing the molecular and physiological mechanisms underpinning plant immune responses to nematode invasion.

Keywords: Effector molecules, Nematode feeding sites, Plant hormones, Plant parasitic nematodes, Secondary metabolites.

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INTRODUCTION

Nearly all life forms on Earth, including humans and other animals, are heavily reliant on plants as their primary source of energy. The escalating human population has necessitated the cultivation of plants to meet its growing needs. Consequently, a substantial portion of Earth's terrestrial landscape has been repurposed by humans to cultivate crops essential for human sustenance, leading to significant advancements in food production. However, since Earth is inhabited by a multitude of organisms, not just humans, the reliability of continuous food production remains uncertain. This is partly due to the presence of pests—defined here as any organism, including pathogens—that can detrimentally impact plant growth, defense mechanisms, and nutritional quality [1, 2]. Annually, pests are responsible for over 40% of global crop losses (IPPC Secretariat, 2021). While the term 'pests' encompasses a broad range of organisms, these entities primarily compete with humans for food and habitat. Both invertebrate and vertebrate pests inflict considerable damage to crops. Although pesticides are commonly employed for pest management, their application often entails substantial costs, including biodiversity loss and ecological harm, which may outweigh the immediate benefits of crop protection [3]. Among the myriad pests, insects, and nematodes are recognized as two of the most prominent groups responsible for significant crop yield reductions worldwide.

NEMATODES AS PLANT PARASITES

Nematodes exhibit extraordinary adaptability, thriving in diverse environments such as deserts, marshes, oceans, tropical regions, and even Antarctica, as they have been reported from every continent. These organisms encompass a variety of life forms, including free-living parasites, fungivores, bacterivores, and even nematophagous (nematode-eating) species. Despite their diminutive size and the challenge of species identification, nematodes hold a pivotal role in ecosystems. Estimates suggest that the global nematode species count could exceed 500,000, although only about 29,000 species have been formally described to date [4]. Their diversity and abundance are second only to insects among multicellular organisms. While many nematodes are parasitic to plants and animals, a significant number are free-living and feed on bacteria, fungi, protozoans, and other nematodes. Currently, there are approximately 4,100 recognized plant parasitic nematode (PPN) species, primarily targeting plant roots, though some also infest aerial plant parts. These PPNs account for roughly 15% of all known nematode species [5, 6]. Although nematode diversity is vast, only a few species cause substantial agricultural damage. Jones *et al.* [7] identified the 11 most critical nematode genera affecting crops, including *Meloidogyne*, *Heterodera*, *Globodera*, *Pratylenchus*, *Radopholus*, *Ditylenchus*, *Bursaphelenchus*, *Rotylenchulus*, *Xiphinema*, *Nacobbus*, and *Aphelenchoides*. Collectively, these PPN species are responsible for annual agricultural losses exceeding $358 billion worldwide [8].

To manage these pests, large quantities of nematicides are used. The global nematicide market was estimated at $1.58 billion in 2022, with projections suggesting it could grow to $4.28 billion by 2032. The Asia Pacific region is expected to experience the fastest market growth during this period [https://www.sphericalinsights.com]. Effective nematode management is highly challenging due to the difficulty in diagnosing above-ground symptoms of nematode infestation. Therefore, an integrated management approach that combines chemical treatments, cultural practices, biological control, and resistant plant varieties is essential [5]. Numerous nematicides, such as aldicarb, carbofuran, fenamiphos, oxamyl, and methyl bromide, have been employed to control nematode populations by disrupting their nervous systems, causing paralysis and death. Despite the challenges associated with commercializing bionematicides, various biopesticides, particularly those utilizing bacterial and fungal antagonists, have shown promise. Plant nematologists have invested considerable effort into understanding the mechanisms of plant defence against PPNs, including the synthesis of metabolites with anti-nematode properties, known as anti-nematode phytochemicals (ANPs).

Plant parasitic nematodes possess unique abilities to detect and respond to chemical signals from their hosts, enabling them to locate and infect plant tissues. Over evolutionary time, plants and nematodes have co-evolved, developing mechanisms to either parasitize or defend against each other. Understanding the complex molecular signalling and interactions during the early stages of host-parasite relationships is crucial for identifying vulnerable points in the nematode lifecycle and disrupting nematode-host recognition. Nematode infestations can significantly reduce crop yields by invading plant roots, altering root architecture, and diminishing the plant's ability to absorb nutrients and water.

FEEDING STRATEGIES OF PLANT PARASITIC NEMATODES

Diagnosing nematode infections based solely on above-ground symptoms can be challenging, as these symptoms often mimic those of nutrient deficiencies. Plant parasitic nematodes primarily feed on plant roots, but they can also parasitize stems, leaves, flowers, and seeds. Despite their diverse feeding strategies, all nematodes utilize a specialized structure called a stylet, located in their stoma, to pierce plant tissues. The stylet's morphology is critical for taxonomic identification and provides insight into the nematode's feeding habits. Fewer nematodes feed on above-ground plant parts such as leaves, stems, and bulbs.

CHAPTER 6

Environmental Factors Influencing Phytochemical Production for Enhanced Phytochemical Defense

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Abstract: Phytochemicals are essential compounds in plants that serve as advanced defense mechanisms against various environmental stressors. This chapter delves into the environmental factors influencing phytochemical biosynthesis, providing a thorough analysis of how plants adapt to different stress conditions. Both abiotic and biotic stressors have a significant impact on phytochemical production. Abiotic stressors, such as temperature fluctuations, variations in light intensity and spectrum, water availability, soil conditions, and salinity, can distinctly modify phytochemical profiles. Extreme temperatures can alter the composition of phytochemicals, while light conditions, including photoperiod and wavelength, regulate the synthesis of crucial compounds. Water stress, from drought or waterlogging, affects phytochemical compositions, and soil factors like pH and nutrient levels influence the overall phytochemical profile. Saline environments induce osmotic stress, leading to notable changes in phytochemical production. Biotic stressors, including pathogen attacks, herbivory, and competitive interactions, also significantly impact phytochemical synthesis. Plants generate induced defenses in response to pathogens, and secondary metabolites play a crucial role in deterring herbivores. Competitive interactions, such as allelopathy, influence phytochemical production, highlighting the complexity of plant responses in competitive settings. The chapter also explores methods to enhance phytochemical production through environmental modulation. Agricultural practices like crop rotation, intercropping, and organic farming can boost phytochemical content. Controlled environment agriculture, such as greenhouse and hydroponic systems, optimizes conditions for superior phytochemical synthesis. Additionally, genetic and biotechnological advancements, including genetic engineering, plant breeding, and the

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use of elicitors and biostimulants, offer promising avenues for increasing phytochemical yields. Future research should focus on refining agricultural practices, optimizing controlled environments, and leveraging genetic and biotechnological innovations to enhance phytochemical production, promoting sustainable agriculture and strengthening plant resilience.

Keywords: Abiotic stress, Biotechnological advancements, Biotic stress, Controlled environment agriculture, Phytochemicals, Phytochemical biosynthesis, Plant resilience.

INTRODUCTION

Plants constantly face a dynamic and often hostile environment, contending with numerous biotic stresses such as attacks from bacteria, fungi, viruses, insects, and herbivores, as well as abiotic stresses including UV radiation, drought, and soil contaminants [1]. In response, they have evolved a sophisticated array of phytochemicals that act as their natural defense mechanisms. Plants, despite being stationary, have evolved to produce a vast array of secondary metabolites. These organic compounds, while not directly involved in primary growth and development, play crucial roles in the survival and resilience of plants [2]. These phytochemicals serve various ecological functions, primarily in plant defense, and encompass a diverse range of classes such as alkaloids, phenolics, terpenoids, and flavonoids, each uniquely contributing to plant defense strategies. Phytochemicals form the first line of defense against pathogen invasion and herbivore feeding through multiple mechanisms [3]. Some possess direct antimicrobial properties, while others work indirectly by attracting beneficial organisms or inducing systemic resistance within the plant [4]. Additionally, these compounds help plants cope with environmental stresses by mitigating UV radiation damage, detoxifying harmful substances, and enhancing nutrient uptake. Understanding the multifaceted roles of phytochemicals in plant defense not only illuminates the complex ways plants interact with their environment but also paves the way for agricultural innovation. Harnessing the natural defensive properties of phytochemicals can foster the development of more resilient crops, thereby reducing reliance on synthetic pesticides and promoting sustainable agricultural practices. Thus, the study of phytochemicals is crucial for ensuring food security and environmental sustainability in the face of global challenges.

Secondary metabolites, which are mainly classified into phenolics, terpenes, and nitrogen/sulfur-containing compounds, are essential for plant defense against predators and pathogens. Terpenes, constructed from 5-carbon isoprene units, function as toxins to deter herbivores. Phenolics, synthesized *via* the shikimic acid pathway, bolster the plant's defense mechanisms. Additionally, nitrogen and sulfur compounds, which derive from amino acids, contribute significantly to plant protection. *In vitro* studies have confirmed the defensive roles of these metabolites, revealing over 100,000 known compounds involved in plant defense, although the full extent of their diversity remains unclear [5]. Higher concentrations of secondary metabolites typically enhance plant resistance to both biotic and abiotic stresses. However, their production can impose significant costs on plant growth and reproduction [5]. The evolution of induced defense mechanisms, characterized by increased concentrations of secondary metabolites under stress conditions, highlights their structural and functional significance. Numerous studies have identified a wide array of plant compounds with ecological and chemical defensive roles, forming the basis of the emerging field of ecological biochemistry. Exploring phytochemicals in plant defense not only deepens our understanding of plant-environment interactions but also offers valuable insights for developing sustainable agricultural practices and resilient crop varieties. Furthermore, primary metabolites, such as proteins, fats, carbohydrates, and dietary fiber, are essential for energy metabolism and cell structure. In contrast, secondary metabolites, which are non-nutritive, play a vital role in plant-environment interactions, including defense against insects and fungi (Fig. **1**).

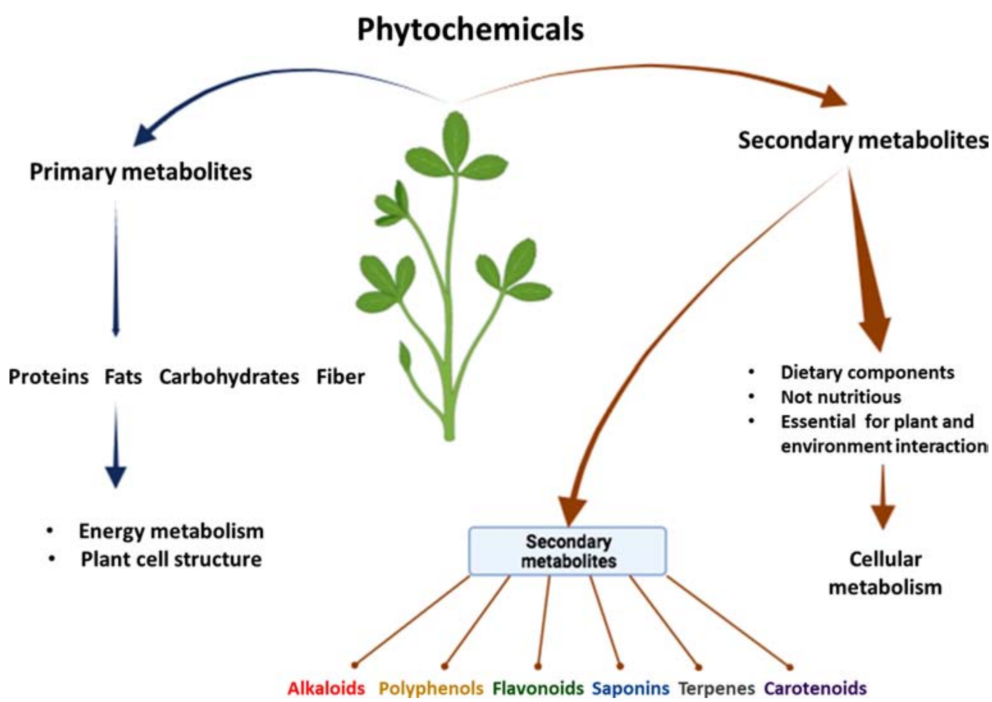

Fig. (1). The difference between primary and secondary metabolites.
(Source: https://doi.org/10.3390/plants13040523).

CHAPTER 7

Exploiting Phytochemicals for Nematode Management as A Control Strategy

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Abstract: Plant-parasitic nematodes, or PPNs, cause significant losses in commercial crops all over the world. Research efforts should be directed toward developing safe and cost-effective control mechanisms due to the health and environmental risks associated with the use of chemical nematicides. An essential component of these initiatives is the wise exploitation of plant-PPN interaction. As research progresses, naturally occurring phytochemicals that are hostile to other nematodes and plant parasites have been discovered. Plants produce a wide range of secondary metabolites that play an excellent role in plant protection. Polythienyls, glucosinolates, isothiocyanates, glycosides, alkaloids, lipids, terpenoids, steroids, triterpenoids, phenolics, and several other classes have been produced by higher plants. This chapter provides insights into the phyto-nematode interactions and production of anti-nematode phytochemicals to protect them from PPNs. Despite being unprofitable in many cases right now, the use of phytochemicals in agriculture has a lot of potential for the future.

Keywords: Alkaloids, Giant cells, Glucoraphanin, Hypersensitivity, Juveniles, Metabolites, Multienzyme, Nematodes, Nematicidal, Plant-parasitic, Resistance, Rhizosphere, Secondary, Stylets, Susceptibility.

INTRODUCTION

The soil region occupying the root area is copious with a broad diversity of microbiomes. The common residents of this area include both plant pathogenic as well as plant beneficial microbiomes [1, 2] Phytoparasitic roundworms causing damage to plants are commonly regarded as plant parasitic nematodes (PPNs) [3]. These PPNs are minute microscopic worms that move around the rhizospheric soil to find their host and finally procure their liquid food material from the plant

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roots [4]. They damage the plants, which results in reduced yields or, sometimes, complete plant losses. About 12.6% of crop losses, which account for 216 billion dollars per year, have been predicted by these PPNs throughout the world [5]. Almost all plant species, including all crops, are parasitized by the more than 4100 PPN species that have been identified to date [6].

Different parasitic modes with varied life cycles have been observed in several forms of PPNs [6]. The major disease-causing agents in crops are phytophagous nematodes, which belong to the order Tylenchida [3]. The members of Tylenchida are even pathogenic to several invertebrate species as well as several fungal species [7]. *Pratylenchus*, *Hoplolaimus*, *Meloidogyne*, *Heterodera*, *Xiphinema,* and *Rotylenchulus* are the most important genera of PPNs responsible for crop damage [8 - 11]. In PPNs, the most flourishing nematodes are sedentary nematodes [12]. The endoparasitic nematode worm, *Pratylenchus penetrans,* is regarded as the causative agent of plant root lesions [13]. They are the active forms and keep on moving through the plant roots in both forms, as adults or juveniles. During the unfavourable conditions inside plant roots, they get away from the roots and roam inside the soil [14]. Other endoparasitic PPNs include the sedentary nematode species *Meloidogyne incognita*. This nematode species is regarded as the root-knot nematode as it forms irregular galls on plant roots. Once the infective stage juvenile (J_2) got into the root, it obtained its diet material near the vascular bundles and underwent development. It then finally loses its moving ability and fixes in one place, forming a gall and completing its life journey inside its roots [11, 15].

The management of these destructive nematodes is quite challenging. Although the use of chemical nematicides has proven effective against these PPNs, they are banned due to their higher cost, low availability, and environmental vulnerability [16 - 18]. In the 20th century, even nematodes have been found to be successful against PPNs, regarded as predatory nematodes. Along with predatory action, they help in nutrient cycling in plants [19]. Recently, more emphasis has been given to the studies of anti-nematode phytochemicals (ANPs) that have been produced by plants to overcome PPN stress [20]. Nematode behaviour, development, reproduction, and survival are influenced by certain plant metabolites secreted from the roots, which minimises plant harm [21, 22]. While there is still little knowledge on how plants alter the nematode community in the rhizosphere, some may even increase nematode-hostile bacteria in the rhizosphere [23, 22]. So, in this chapter, the main emphasis has been placed on the various strategies that plants exhibit (mainly the production of phytochemicals) to defend them from the PPN attack.

PHYTO-NEMATODE INTERACTIONS

A huge variety of crop plants can be completely destroyed by plant-parasitic nematodes, resulting in annual agricultural losses worth billions of dollars [16]. All portions of the plant, including the roots, leaves, stems, flowers, and seeds, are consumed by nematodes. Although nematodes consume plants in a variety of ways, they are all equipped with a unique spear known as a stylet [3]. These phytopathogens drastically alter the appearance and physiology of their hosts [24]. The only food source for all plant parasitic nematodes (PPNs) is the cytoplasm of living plant cells, making them obligatory parasites [25]. Although both cyst and root-knot nematodes engage in intricate interactions with their hosts, their parasitic cycles differ in certain notable ways [26]. After entering roots, cyst nematodes proceed to the vascular cylinder, puncturing cells with their stylets and causing disruptions along the way [27]. They create a feeding site, presumably by injecting stylet secretions. The disintegration of the cell walls separates the original feeding site cell and its surrounding cells, which leads to the growth of a multinucleate syncytium (the establishment of a feeding site) [28]. Before becoming adults, cyst nematodes go through three molts inside the root. They typically procreate sexually, with the female becoming egg-filled after fertilisation [29]. The carcass of the dead female turns into a cyst that shields the eggs.

The juvenile of the root-knot nematode migrates down the plant cortex towards the root tip, moving intracellularly after entering the root [26]. After entering the vascular cylinder's base, the juveniles go up the root [30]. They cause nuclear division in the host cells without cytokinesis, therefore creating a permanent feeding site in the root's differentiation zone [31]. Giant cells, or galls, also known as “root knots,” are created when the plant cells surrounding the feeding site proliferate and enlarge [32]. After three moults, the nematodes transform into pear-shaped, egg-laying females by ingesting the cytoplasm of the large cells generated from plants through their stylets [33, 34].

Upon invasion, these nematodes receive their water and nutrition from feeding cells that are induced to redifferentiate by root-knot and cyst nematodes [35]. Plants use a variety of complementary mechanisms to identify PPN invasion, which in turn stimulates immunological responses to PPN infection [36, 37]. Signal transduction, defence gene activation, and other mechanisms comprise the plant's immunological response to parasitic nematodes [38]. Through the use of cell surface-localised pattern recognition receptors (PRRs), plants are able to identify pathogen-associated molecular patterns (PAMPs) formed from PPNs, which results in pattern-triggered immunity (PTI). The recognition of damage-associated molecular patterns (DAMPs) using PRR-based recognition enables

CHAPTER 8

Current Limitations and Challenges in Utilizing Phytochemicals as Plant Defense Mechanism Against Nematodes

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Abstract: Understanding the dynamic interplay between phytochemicals and nematodes is vital for advancing integrated pest management strategies. Phytochemicals, the naturally occurring compounds in plants, have garnered significant attention for their potential role in defense against plant-parasitic nematodes. These bioactive compounds can deter nematodes through various mechanisms, including toxicity, repellence, and interference with nematode development. Despite promising laboratory results, the practical application of phytochemicals in agriculture faces several limitations and challenges. One major challenge is variability in phytochemicals' production among plant species and even within different parts of the same plant, influenced by environmental factors and genetic variability. Furthermore, the complex interactions between phytochemicals and the soil microbiome can impact their efficacy and stability. Another significant hurdle is the potential for nematodes to develop resistance over time, reducing the long-term effectiveness of these compounds. Additionally, the extraction, formulation, and application methods of phytochemicals must be optimized to ensure they are cost-effective and environmentally sustainable. Addressing these challenges requires multidisciplinary approaches, integrating plant breeding, molecular biology, soil science, and agronomy to develop reliable and robust phytochemical-based strategies for nematode management.

Keywords: Alkaloids, Diarylheptanoids, Flavonoids, Hydroxycinnamic acids, Nematodes, Phytochemicals, Phenolics, Plant defense, Plant parasitic nematodes, Stilbenoids, Tannins.

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INTRODUCTION

Phytopathogens, which are organisms that cause diseases in plants, typically attack during the growth phase, leading to significant disruptions in cellular metabolism and nutrient absorption. These organisms are common in cultivated and postharvest cereals, vegetables, and fruits. Plant-parasitic nematodes (PPNs) rank are amongsome of the most significant agricultural pests, as they reduce crop yields by altering nutrient uptake and provoking secondary infections as well as acting as vectors for viruses and distortion of water transport [1, 2]. While nematode parasitism rarely results in plant death, the impact of PPNs on agriculture is considerable. Though quantifying their exact influence is challenging, estimates suggest that PPNs contribute to a global yield reduction of 10-25% [3]. Around four thousand different species of nematodes that are parasitic to plants were recorded, with the majority feeding on roots and others on above-ground plant components [4]. Despite the high degree of diversity among them, only a few genera within the sedentary PPNs—cyst and root-knot nematodes—cause the great bulk of losses [5]. These nematodes are very hard to control, and management needs a combinative approach comprising some chemical treatments, cultural practices, biocontrol, and planting highly resistant planters, which, however practicable, is additionally crucial [6]. Plant nematologists have devoted significant resources to studying plant defense mechanisms against PPNs to develop innovative control methods. One such strategy involves the synthesis of metabolites with anti-nematode properties [7].

Despite their effectiveness and accessibility, pesticides are commonly used to combat PPNs. However, they have several drawbacks, including the development of resistance and their classification as toxic substances. This toxicity affects not only bacteria, fungi, viruses, protozoa, and nematodes but also poses risks to all living organisms including humans, animals, and the environment [8]. The pesticide usage can result in both acute and chronic toxicity, persisting in the environment and leading to soil and water pollution. Furthermore, their incorporation into the food chain can lead to bioaccumulation and biomagnification. These substances have been linked to various toxic mechanisms, including acting as endocrine disruptors and generating oxidative stress within cells [9]. They have acquired this developmental ability due to the evolution of more advanced secondary metabolism in plants, which allows photosynthetic organisms to synthesize a plethora of metabolites. Plants are thought to produce 200,000 secondary metabolites [10].

OVERVIEW OF KNOWN ANTI-NEMATODE COMPOUNDS (ANPS)

Anti-nematode compounds (ANPs) are categorized into various classes, including saponins, glucosinolates, alkaloids, terpenoids, organosulfur compounds, and phenolic compounds (Fig. **1**). Although some chemicals may fall into more than one category, this taxonomy offers an organized method for comprehending these metabolites. Researchers frequently find that classifying ANPs according to their chemical makeup—which is frequently the same as their plant family—helps in their studies. Each species of plant produces a variety of secondary metabolites, but they often specialize in creating specific protective compounds. An example of this is that plants belonging to the Fabaceae family are known to secrete (iso)flavonoids, but plants in the Solanaceae and Malvaceae families are more likely to produce terpenoid phytoalexins. Glucosinolates are a special class of defense chemicals found only in plants in the Brassicales order. It is clear how different plants have their special chemical arsenal to protect themselves [11]. We will discuss secondary metabolites in this chapter, which are thought to aid plants in nematode defense. These are substances that are present in tissues that have been parasitized by nematodes. They may be continuously present in the plant or may be created in reaction to an infection. A correlation appears to exist between these compounds and resistance to nematodes. Plant extracts include a wide variety of nematicidal chemicals, however, not all of them are involved in interactions between plants and nematodes [12].

Phenolic Compounds

Several PPNs like *Meloidogyne incognita* are usually controlled by a large proportion of many groups of phytochemicals classified as phenolic compounds mostly oriented from the phenylpropanoid pathway (Table **1**). They are regarded as fundamental components in conferring resistance against diseases and pests in plants [13]. Following decades of rigorous investigation, it has been determined that these naturally occurring phytochemicals have a significant role in nematode resistance. Numerous recent research studies have emphasized that higher basal along with induced levels of phenolic compounds are associated with improved resistance to nematodes across various plant-nematode interactions [14 - 16]. L-phenylalanine and, to a lesser extent, L-tyrosine are aromatic amino acids that constitute the primary source of phenolic compounds in plants. The enzyme phenylalanine ammonia-lyase (PAL) deamines L-phenylalanine to produce (E)-cinnamic acid. Cinnamic acid-4-hydroxylase (C_4H) can then hydroxylate this to produce para-coumaric acid. Alternatively, tyrosine ammonia lyase (TAL) can directly create para-coumaric acid by deaminating L-tyrosine. The reactive intermediate para-coumaroyl-CoA is created when acetyl coenzyme A and para-coumaric acid are combined by 4-coumarate-CoA ligase (4CL). The

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Dr. Shivam Jasrotia, Ph.D. in life sciences (zoology) from Guru Nanak Dev University, Amritsar, is a distinguished academic and researcher in the field of nematology. With over eight years of teaching experience, formerly with the Jammu and Kashmir Higher Education Department and currently at Chandigarh University, Prof. Jasrotia is a passionate educator and researcher. His research focuses on plant pathology, particularly the bio-management of nematodes as sustainable alternatives to chemical nematicides. He has published over 25 research papers in reputed journals, with more than 3,000 citations, an h-index of 13, and an i10-index of 15. He has actively participated in numerous national and international conferences, seminars, and workshops, sharing his insights and advancing knowledge in his field. His academic rigor and dedication to eco-friendly solutions underscore his reputation as a leading voice in sustainable agricultural science. Beyond academics, he has made notable contributions to extracurricular and co-curricular development by organizing a variety of intra- and interdepartmental events at the university level, reflecting his commitment to holistic student development and campus engagement.

Ajay Kumar

Dr. Ajay Kumar did a Ph.D. in life sciences from Guru Nanak Dev University, Amritsar. He has been a UGC-BSR fellow and a qualified UGC-NET. He worked as a senior project associate at Punjab Biotechnology Incubator, Mohali, and as a postdoctoral fellow at the University of Wisconsin, Madison, USA. Currently, he is an assistant professor at the University Centre for Research and Development (UCRD), Chandigarh University, Mohali. His research focuses on cancer chemoprevention using natural products. He has more than 35 publications in high-impact journals and 10 book chapters with more than 700 citations, h-index of 15 (Google Scholar), and i10-index of 19 (Google Scholar). He has presented at various international conferences and is a life member of the Environmental Mutagen Society of India.