Mohd. Sayeed Akhtar Editor

Opportunistic Fungi, Nematode and Plant Interactions

Interplay and Mechanisms



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This book is dedicated to



Abdul Ghaffar Khan (1890–1988) (Frontier Gandhi)

Freedom fighter who fought for injustice with sadbhavana, and founder of Khudai Khitmatgar

Foreword



Opportunistic fungi play a significant role in plant-nematode interactions. They can both positively and negatively impact the interactions between fungi and nematodes, as well as influence plant diseases. Fungi can attract or repel nematodes; nematodes can feed on fungi, acting as biological controls for plant diseases while simultaneously inducing suppressiveness in agricultural soils, affecting cyst and root-knot nematode population dynamics. Nematode feeding sites, such as syncytia or giant cells, provide favorable conditions for fungi to enter and infect host plants. The nematode-instigated physiological changes can at the same time promote various phases of fungal life cycles, such as germination, development, and reproduction. Opportunistic fungi are commonly found in the soil or in decomposing organic material and in their interaction with plant nematodes, these can engage in various modes, including direct parasitism or the infiltration of the nematode body for the purpose of tissue consumption. Occasionally, they produce toxins or enzymes that are capable of eliminating or debilitating the nematode, thereby rendering it more susceptible to other predatory organisms. Moreover, opportunistic fungi can contribute to safeguarding plants from nematode infection by out-competing the nematodes for resources and living space. The interaction between opportunistic fungi and nematodes is characterized by complexity and is contingent upon the particular species involved as well as the prevailing environmental conditions. For instance, *Fusarium oxysporum*, a pathogen responsible for causing wilt disease, as well as Trichoderma harzianum, a biocontrol fungus, possess the ability to parasitize rootknot nematodes. In contrast, Paecilomyces lilacinus parasitizes root-knot nematodes, cyst nematodes, and lesion nematodes. Overall, the interactions between opportunistic fungi and plant nematodes are complex and can have significant implications for plant health and disease management in agricultural ecosystems.

This book volume titled *Opportunistic Fungi*. Nematode and Plant Interactions: Interplay and Mechanisms includes 11 chapters contributed by academicians, scientists, and researchers from different parts of the world. Chapter 1 focuses on different opportunistic fungi, nematode interactions on host plants and their mechanisms of actions, whereas Chaps. 2 and 3 discuss the interaction between the opportunistic fungi, plant, and nematode in agricultural and vegetable crops. In Chap. 4 contributors highlight the biochemical changes in host-plant invaded by opportunistic fungi and nematodes, whereas Chap. 5 discusses the response of ROS in host-plant assaulted by opportunistic fungi and nematodes. The functions of flavonoids in plants, pathogen, and opportunistic fungal interactions have been evaluated in Chap. 6, whereas the occupancy of flavonoids in plants, pathogen, and opportunistic fungi interactions is outlined in Chap. 7. The mode of interactions between opportunistic fungi, nematodes, and other soil microbiota has been discussed at length in Chap. 8, whereas the molecular interactions and recent developments between the opportunistic fungi, nematodes, and plants are given in Chap. 9. Chapter 10 highlights the involvement of parasitism proteins in plant nematodes and opportunistic fungi connections. The role of lifestyle pattern and soil microbiome interaction of arthrobotrys species for the biostimulant production are summarized in Chap. 11.

This book covers the basic and applied aspects of opportunistic fungi and nematode interactions, physiological and molecular changes in host and pathogens, as well as mechanistic aspects. It has been written with the great aim of proving highly beneficial to academicians, researchers, and students.

Faculty of Science Ege University, İzmir, Turkey Münir Öztürk

Preface

Plant parasitic nematodes (PPNs) are documented as the most destructive pests for numerous economically important crops worldwide. According to an estimate, the average crop lost caused by this notorious pest is about 12.3%. Over the past few decades, chemical nematicides have been frequently used for the management of nematode diseases; however, general concerns about human health and environmental safety have led to restrictions on chemical nematicides applications for the control of PPNs. Cultural practices are also used for nematode management, but extensive annual losses in crop yields and quality demonstrate a crucial need for an ecofriendly and environmentally safe approach that provides better management of PPNs.

Soil serves as an excellent niche for a diverse range of microorganisms. The microorganisms lying in the rhizosphere have the capability to act as frontline warriors against the pathogen attacks on root. Among the different types of beneficial rhizospheric microorganisms, opportunistic fungi (OP) such *as Arthrobotrys, Cylindrocarpon, Fusarium, Paecilomyces, Plectosphaerella, Pochonia, Rhizoctonia,* and *Trichoderma* are of prime importance and might play a very significant and crucial role in the management of plant diseases caused by PPNs. OP have the ability to directly parasitize PPNs by secreting metabolic compounds that affect the viability of one or more stages of the nematode life span, with obese female or cysts becoming highly susceptible to these fungi. Since opportunistic fungi and PPNs both share the common ecological niche and influence plant growth, it is a bit tough to generalize the series of events taking place during this underground assembly in one plane, but the recent development of sophisticated molecular tools has provided an impression of the interaction taking place between OP fungi, PPNs, plants health, and sustainable environmental conditions.

The present book *Opportunistic Fungi*, *Nematode and Plant Interactions: Interplay and Mechanisms* is a timely effort in the direction of describing the opportunistic fungi, nematode and plant interactions, fungal behavior and etiology, their management strategies, and the mechanisms involved against the unseen enemies. This book volume consists of 11 chapters from renowned scientists and scholars throughout the globe who contribute basic and applied aspects of opportunistic fungi and nematode interactions, physiological and molecular changes in hosts and pathogens, and mechanistic aspects. Besides this, the book also provides valuable information for students, teachers, and professionals involved in research related to plant pathology, ecology, soil science, host-plant interactions, and microbial ecology. I am highly grateful to all our contributors for readily accepting our invitation to not only share their knowledge and research but also venerably integrate their expertise in dispersed information from diverse field in composing the chapters, and enduring editorial suggestions to finally produce this venture. I greatly appreciate their commitment. I am also thankful to Professor Munir Ozturk for his suggestion and writing the foreword for this volume. We also thank the team at Springer International, especially Rhea Dadra, Priyanga Kabali, and Sanchi Bhimrajka, for their generous cooperation at every stage of the publication.

Shahjahanpur, Uttar Pradesh, India

Mohd. Sayeed Akhtar

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About the Editor



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Interactions of Opportunistic Fungi, Plants, and Plant Parasitic Nematodes

Mohammad Danish and Merajul Islam Robab

1.1 Introduction

Agriculture output in India has declined for a variety of causes. Diseases are a severe impediment to agricultural cultivation. One of these is plant parasitic nematode (PPN) infestation, which reduces crop quality and production. PPNs drastically impair crop harvest as well as yield, which is a huge financial concern for the world's farming sector (Shakeel et al. 2022). Due to their microscopic size, concealed habitats, and absence of obvious symptoms on the aerial parts of the plants, plant parasitic nematodes are regarded as a hidden enemy of crops. PPNs infiltrate the roots of the plant, where each nematode creates a feeding location (Pervez and Ali 2011). This complex developmental process results in significant modifications to root structure and metabolism, including the development of root galls, syncytia, large cells, lesions, etc. (Danish et al. 2021). Nematodes cause an estimated \$100 billion in losses to agriculture every year (Coyne et al. 2018). There is an urgent need to control these plant parasitic nematodes using appropriate treatments, given the monetary losses brought on by root-knot nematodes.

Chemicals, host plant resistance, crop rotation, soil solarization, antagonistic organisms, etc. are only a few of the methods that have been utilized to control them thus far. The most popular method of nematode control is crop rotation, although this method needs enough space to grow crops that are not nematode hosts. Also, the grower must make good revenues from these alternative crops. Chemical

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treatments have been found an effective controlling method against nematodes, but due to their scarcity, high cost, and transient effects, nematodes developed a resistance to them (Chen et al. 2020). Additionally, these treatments can destroy beneficial microorganisms, and prolonged chemical compounds may pose notorious risks to the ecological integrity (Dong et al. 2006). Nematicides may be extremely poisonous to animals and harmful to the developing foetus (Sharma and Rakesh 2009). Thus, it is imperative to create affordable and environmentally acceptable agents due to restrictions on the use of nematicides. To combat and minimize the detrimental effect of nematodes on crop ecosystems, biocontrol agents such as fungi in particular have the potential to be a promising alternative to nematicides and conventional techniques (Danish et al. 2022).

The importance of employing fungi as biological control agents against plant pathogen has substantially increased since fungi reproduce rapidly, selectively, and both sexually and asexually including target specific activity. They also have a short generation time. Also, they can continue to exist sustainably in the absence of the host by transitioning from parasitic infection to saprotrophism (Thambugala et al. 2020). Opportunistic fungi, parasites of nematode eggs, parasites of nematode cysts, and fungi that produce nematode toxic chemicals are examples of nematode opponents. Surprisingly, fungus from quite different orders and families can be found in each of these groups. While fungal infections cause plant physiology to suffer, mutualistic fungi aid hosts in their defence against infection and pests. Fungi produce bioactive compound such as short peptide signalling pathways, enzymes, and bioactive compounds, which encourage invasion and contribute to both symbiotic as well as detrimental connections (Zeilinger et al. 2016). Especially those that can be achieved via induced systemic resistance (ISR) induction are the most important beneficial fungi with biocontrol ability, such as arbuscular mycorrhizas, ectomycorrhizas, endophytes, Trichoderma species, and yeasts (Ghorbanpour et al. 2018). Therefore, this chapter focuses on different opportunistic fungi, nematode interactions on host plants and their mechanisms of actions.

1.2 Interaction of Plant Parasitic Nematodes with Different Fungi and Plants

1.2.1 Trochoderma Spp.

Numerous species of *Trichoderma* spp. commonly live in the soil, rhizosphere, and endosphere of plants. These fungi have caught our interest because they can inhibit the development and spread of potential infections like nematodes and fungus (Poveda 2021). In compensation for plant-derived sugars, *Trichoderma* spp. have been viewed (mainly) as non-pathogenic and opportunistic plant symbionts that can colonize plant roots and interact favourably with their hosts through *Trichoderma* effector proteins and hormonal crosstalk (Guzmán-Guzmán et al. 2019). As a result of the interaction between *Trichoderma* and plants, the plant gains not only an increase in biomass and general nutrition but also defence against a number of

phytopathogens, either directly by acting as a mycoparasite and competing with the pathogen for nutrients or inadvertently by triggering the plant defence system (Mukherjee et al. 2022). Many species of this genus have been investigated under the greenhouse as well as in the field conditions for their biocontrol potentials (Alfiky and Weisskopf 2021). T. harzianum inoculation on tomato seeds reduced the level of infection brought on by the nematode *Meloidogyne javanica* in greenhouse conditions, impacting the establishment, reproduction, and nematode development (Sahebani and Hadavi 2008). Also, they observed a significant decline in egg hatching, indicating that Trichoderma species has a lot of potential as a biocontrol agent for this nematode. Moreover, T. harzianum can promote immunity against nematodes and other diseases. T. harzianum increases the gene expression of PR1, PR5, JERF3, and ACO, which are connected to SA- and JA/Et-mediated defence responses in plants, and reduces the symptoms of infection brought on by the nematode M. incognita in tomato plants (Leonetti et al. 2017). Furthermore, they noted that second juveniles of Heterodera avenae eggs and second-stage juveniles are susceptible to parasitization by T. longibrachiatum T6, which decreases the nematode's survival. T. longibrachiatum T6 enhanced flavonoid and lignin content, as well as defence-related enzyme activity in wheat roots in a greenhouse experiment, imparting resistance against the nematode H. avenae (Zhang et al. 2017). Although, field applications should be handled with caution given that it is the only member of the genus Trichoderma to have been identified as an opportunistic human pathogen thus far. According to Pathak et al. (2005), using T. virens or T. harzianum 1 week before nematode inoculation at 4 and 8 g/kg soil considerably decreased the nematode parameters in soil compared to control. According to Devi et al. (2002), T. viride or T. harzianum added in soil at 1 g/kg increased plant growth and decreased M. incognita population. According to Goswami and Mittal (2004), T. viride culture filtrates were highly toxic against J_{2} s of *M. incognita* that were infecting tomato plants. They also demonstrated that T. viride culture filtrates were also effective at preventing M. incognita eggs from hatching. Trichoderma species use a variety of strategies to combat plant diseases, including mycoparasitism, competition, inducing host plant resistance, and antibiosis (Zeilinger et al. 2016).

1.2.2 Ovicidal and Larvicidal Fungi

Pochonia chlamydosporia has been discovered in nematode suppressive soils to parasitize eggs and has a global distribution. According to Giné et al. (2016) *P. chlamydosporia* is the primary biotic component causing soil suppressiveness to root-knot nematodes (RKN) in horticultural crops. In the absence of both plant and nematode hosts, the fungus is still able to survive as a saprophyte in soil. The fungus can colonize host plant roots in the rhizosphere, and certain *Pochonia* species have even been noted to exhibit endophytic activity in some plants belong to Poaceae and Solanaceae family—a growth habit that may aid the host plant's defence against soil-borne infections (Maciá-Vicente et al. 2009). The fungus is also a direct and indirect opponent of RKN and cyst nematodes, acting by parasitizing eggs. *P.*

chlamydosporia field populations can include individuals that perform a variety of highly advantageous functions for plants, such as promoting plant growth that increases tolerance of plants, inducing plant defence mechanisms that control infection, growth, and reproduction of RKN, effective egg parasites that suppress the RKN inoculum, or saprophytic behaviour that contributes to the organic matter cycle and plant nutrition (Ghahremani et al. 2019). There have been reports of *P. chlamydosporia* induced plant defensive mechanisms against RKN, including a rise in the activity of defence enzymes such as peroxidases (POX) and polyphenol oxidases (PPO) enzymes at the stage of root nematode invasion within the 2–3 days of nematode inoculation. The effect of local defence mechanisms alone, however, might not be sufficient to achieve significant nematode suppression because *P. chlamydosporia* does not extensively colonize the root (Escudero and Lopez-Llorca 2012), even though this is improved by chitosan irrigation.

1.2.3 Paecilomyces Spp.

Different species of genus "Paecilomyces" can be discovered in a variety of environments, such as nematodes suppressive soil (Aminuzzamana et al. 2013) and in the root zone of different plants (Kilama et al. 2007). Paecilomyces also contributes significantly to the development of many plants as an endophyte by offering a number of benefits. Both directly and indirectly, it has the ability to act as a biostimulant. Paecilomyces or metabolites secrete by them improve agricultural output and plant morphological characteristics when used directly (Moreno-Gavíra et al. 2020.) Paecilomyces is a nematophagus fungus that has undergone extensive research and can be found in many different biological formulations that are utilized in agriculture (Dong et al. 2007). By several pathways, the interplay between plants and Paecilomyces enhances plants growth and offers defence against plant pathogens (Malhadas et al. 2017). Paecilomyces has positive impacts on crop growth when employed against nematodes pathogens by acting as a biological agent (Mezeal et al. 2018). This predatory fungus is common in many types of soils. The root zone can be inoculated with this fungus to encourage plant development and reduce nematode infestation. There are numerous instances when Paecilomyces species act against the nematodes, particularly when dealing with Meloidogyne species, including other genera such as Pratylenchus, Globodera, Rotylenchulus, Heterodera (Lima-Rivera et al. 2016). The treatment of P. lilacinus under greenhouse and field conditions has efficiently controlled root-knot and cyst nematode (Moreno-Gavíra et al. 2020). Plants treated with P. lilacinus exhibit decreased root galling as well as improved plant development and yield in soils containing root-knot nematodes (Mittal et al. 1995). The use of P. lilacinus reduces both the overall population of nematodes in the soil and the hatching of egg masses.

The genus *Paecilomyces* has many species that produce a broad range of secondary metabolites, including nematicidal, with various chemical compositions and biological activity (Lima-Rivera et al. 2016). Eggs containing younger *M. hapla* larvae were far more susceptible to the serine proteases generated by *P. lilacinus* than eggs containing older, more mature larvae. The penetration of the nematode cuticle and subsequent cell breakdown are shown to be facilitated by a variety of hydrolytic proteins, including proteases mainly serine proteases, collagenases, and chitinases (Paul et al. 2013). Similar to this, many secondary metabolites released by *Paecilomyces* are important in biological control of nematodes (Yan et al. 2011). The members of this genus, notably *P. lilacinus*, can enter both the eggshells and structural components of the juvenile and adult stages of various species of nematodes via spore germination, hyphal branching, and appressoria formation (Khan et al. 2006). The synthesis of various enzymes such as amylases, lipases, proteases, and chitinases showing nematicidal effect has been described by (Giné and Sorribas 2017). The virulence and parasitic capacity of *P. lilacinus* against *M. incognita*, *Panagrellus redivivus*, and *Caenorhabditis elegans* are increased by the overexpression of genes that control the synthesis of all these enzymes (Wang et al. 2014).

1.2.4 Nematode-Trapping Fungi

Nematode-trapping fungi are a distinct and fascinating genus of fungi that capture and kill nematodes using specialized trapping structures. They can develop a variety of trapping methods, including constricting rings, adhesive networks, and adhesive mycelium (Jiang et al. 2017). In a variety of crop species, nematophagous fungi are well-known bio-agents that are effective against a wide range of nematode pathogens (Singh et al. 2013). The ability of A. oligospora directly or indirectly encourages plant development (Danish et al. 2022). Reduced nematode pathogens in the rhizosphere and root systems are necessary for the direct effects to occur. The production of metabolites, improvement of other soil microbial flora, and manipulation of root secretion systems are indirect effects that have an impact on plant growth by reducing the growth and reproduction of phytopathogens and other harmful microorganisms. The use of A. oligospora appears to favour the promotion of plant development, the management of disease, and the induction of systemic resistance (Singh et al. 2012). The use of A. oligospora against M. incognita in Withania somnifera resulted in a considerable decrease in the nematode population and an increase in plant growth, as demonstrated by Sharma and Pandey (2009). In vitro parasitism of five A. oligospora isolates against M. graminicola was assessed by Singh et al. (2012) demonstrated that A. oligospora isolate VNS-1 killed nematode larvae (J_2) in 8 days. They reported that, when A. oligospora was applied to rice plants that had been inoculated with M. graminicola, the number of galls decreased and plant growth increased. According to Simon and Anamika (2011), the addition of A. oligospora to M. graminicola infested soil decreased the frequency of root galls while also promoting rice plant growth. In tomato plants infected with M. javanica, A. oligospora dramatically reduced the mean numbers of galls, egg masses, and eggs per egg mass (Singh et al. 2007; Sharma and Pandey 2009; Jamshidnejad et al. 2013). Similarly, Sharf et al. (2014) conducted the research on P. chlamydosporia against M. incognita in red kidney beans, and the results showed that P. chlamydosporia dramatically decreased the number of gall and number of egg masses and improved plant growth.

Following mechanism behind the capturing ability, it was discovered that *A. oligospora* produce two pathogenicity factors: an extracellular serine protease and a carbohydrate-binding protein (lectin) (Yang et al. 2007). Extracellular proteases are crucial in the degradation of nematode structural elements. *A. oligospora* captured nematodes have been reported to be immobilized by proteases (Tunlid et al. 1994). The amount of extracellular proteases produced by nematophagous fungi is associated with their capacity to eradicate nematodes; the greater their output, the more effective they are at eliminating nematodes (Bedelu et al. 1998).

1.2.5 Mycorrhizal Fungi

Arbuscular mycorrhizal fungi are thought to colonize more than 80% of all terrestrial plant species. They are obligate root symbionts. In exchange for the photosynthetic carbon from their host, they boost nutrient intake, which promotes plant development (Smith et al. 2010). Moreover, they can reduce plant stress brought on by both biotic and abiotic causes, such as plant parasitic nematodes (Vos et al. 2012). As previously discussed by Hol and Cook (2005), AMF can also reduce population density of pant parasitic nematodes. AMF possesses anti-PPN properties in plants such as banana, coffee, and tomato, study performed under in vitro, greenhouse, and in field experiments (Koffi et al. 2013). Reduction in root penetration of tomato plant by the false root-knot nematode (Nacobbus aberrans) were noted by the application of Rhizophagus intraradices and Funneliformis mosseae (Marro et al. 2018), and G. intraradices, G. mosseae, and G. etunicatum decrease M. javanica population in peach trees (Calvet et al. 2001), have all demonstrated a reduction in nematode population by enhancing the host nutrient status. The effectiveness of AMF on plant nematode populations and their capacity for infection depends heavily on regional environmental factors. Changes in potassium, phosphorus, and moisture are the main factors affecting the positive effect produced by mycorrhizal fungi in this regard (Ferreira et al. 2018). AMF-mediated biocontrol can occur through a variety of mechanisms, including direct effects of AMF on the pathogen, such as competition for resources or habitat, or indirect effects transmitted by plants. The latter group includes the effects of AMF on plant tolerance, plant defence induction, and altered plant exudation, which results in changed rhizosphere associations. The various systems are not completely independent of one another, and biocontrol is most likely the result of a combination of multiple mechanisms (Cameron et al. 2013). Furthermore, the proportional importance of a certain route can fluctuate based on the specific AMF-pathogen-plant relationship. There has been significant advancement in recent years, particularly in the fields of induced systemic resistance (ISR) (Pieterse et al. 2014) and the function of the rhizosphere in biocontrol (Cameron et al. 2013). Its use as biological control agents in the field is relatively uncommon in agriculture, despite several publications on the biocontrol effect of AMF (Salvioli and Bonfante 2013). Performance variations based on the AMF

isolate, pathogen, plant type, and environmental conditions are partly to blame for this (Salvioli and Bonfante 2013). The effectiveness of these biocontrol agents will therefore be improved with a better understanding of how they work.

1.3 Conclusions and Future Prospects

A lot of research has been done on the interactions between crop, nematode, and fungal species in both glasshouse and field conditions to gain the comprehensive knowledge in reducing plant parasitic infections, on different crop plant by applying biocontrol fungi. It was most probable that these fungi have a biocontrol effect in conjunction with increased host tolerance, organism competition, and systemic resistance. The inherent mechanisms governing ecosystem stability under field circumstances may be one of the causes of the variations between laboratory-based and field-based trial findings. Before using fungi in the field, case-by-case study will be necessary because the biocontrol effect depends on a number of factors, such as the species involved. It is necessary to conduct more research, including studies into induced systemic resistance and metabolome changes, to better understand the processes underlying how these fungi affect nematode population densities and promote plant growth. Further research on the interactions between fungi and nematodes in crop hosts is necessary because there is a lack of insight about their effects in the rhizosphere. Thus, by comprehending how organismal interactions in native niches are controlled, we may be able to improve applications that take into consideration native agricultural ecosystems and eventually result in sustainable crop protection techniques that preserve biodiversity.

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