Review Article

Mechanism of Antagonistic Bioagents in Controlling of Root-Knot Nematodes (*Meloidogyne* sp.): A review

Abstract

Root-knot nematodes are among the most significant pathogenic organisms due to their global distribution, capacity for destruction, and economic importance. Antagonistic bioagents are a more effective alternative to synthetic pesticides in the suppression of root-knot nematodes. Bioagents reduce the use of synthetic chemicals, which are hazardous to both humans and the environment. Despite this, some bioagents, such as fungi and bacteria have unknown mechanisms. This review discusses the nematophagous bacteria and fungi that have been discovered so far, including *Pochonia*, *Trichoderma* sp., *Pseudomonas* sp., and *Bacillus* sp., with an overview of the current advances in research regarding their molecular and biochemical control mechanisms. Biological control agents (BCAs), as valuable ecological enemies of nematode infestations, use a range of mechanisms, such as parasitism, nutrient competition, toxin production, induce systemic resistance to antibiotics, enzymes, and enhance plant health. They suppress nematodes directly, improve plant growth, and facilitate the colonization and activities of antagonistic microbes in the rhizosphere. Understanding the molecular basis of BCAs suppression mechanisms provides the basis for their future incorporation into phytopathogen or plant disease control management. This study reviews the current threat posed by the root-knot nematode, biological control, antagonistic bioagents, and their mechanisms, and the future perspectives in modern agricultural sustainability to provide a basis for the broad control of root-knot nematodes.

Keywords: Root-knot nematodes, biological control, mechanism, biological control agents, plant-parasitic nematodes

Introduction

Plant-parasitic nematodes (PPNs) are among the most dangerous plant pathogens, exacerbating plant diseases and interfering with crop development, contributing to economic losses (Subedi *et* *al*., 2020; Ahmad *et al*., 2021). PPNs, or Phytonematodes, are parasitic worms that spend part of their lives in the soil, causing damage to plant tissues while feeding (Sato *et al.*, 2019). They are also known to attack diverse portions of vascular plants, with the majority feeding on or in plant roots and the minority feeding on aerial parts (Misgana 2018). PPNs are major threats to the world's food supply, accounting for at least 12.3% of global food production loss each year (Singh *et al.,* 2019). One of the most significant worms associated with PPNs is the root-knot nematode (*Meloidogyne* sp.). Root-knot nematode (RKN) is the most significant PPN species on the planet and is among the top five primary plant pathogens (Abd-Elgawad, 2020; Karuri *et al.*, 2017; Mukhtar, 2018). Of these, the root-knot nematodes are possibly the most important because of their global distribution, destructive capacity, and economic importance (Khan *et al.*, 2020). They are thought to be the most dangerous nematodes on the planet. They affect over 5000 plant species and cause economic losses in a variety of crops (Costa *et al.*, 2019; Perpétuo *et al.,* 2021). Worms are widely regarded as the most damaging eggplant pests (Aydinli and Mennan, 2016). *Meloidogyne incognita, M. arenaria, M. hapla,* and *M. javanica* are the most common species of phytophagous RKNs in the genus *Meloidogyne* (Mukhtar and Hussain, 2019; Murata *et al.,* 2020; Leong *et al.,* 2021). *Meloidogyne* sp. threatens over 2000 plant species, including tobacco (*Nicotiana tabacum*), coffee (*Coffea arabica*), tomato (*Solanum lycopersicum*), Niebe (*Vigna sinensis*), kenaf (*Hibiscus cannabinus L.*), sugar cane (*Saccharum officinarum*), tea (*Camellia sinensi*), carrot (*Daucus carota*), melon (Lima *et al.,* 2017). Chemical nematicides and resistant cultivars have traditionally been used to manage *Meloidogyne* sp. (Jones, 2016). Synthetic agrochemicals, which are made up of inorganic or organic compounds, have been the most successful technique in modern agricultural production for controlling plant diseases and pathogens, protecting crop quality, and increasing production because of their affordability, easy handling, and efficacy. While nematodes can be effectively managed with nematicides, their use is restricted because of their limited-term consequences: increased prices, nematode resistance establishment, environmental and health risks, toxic effects, and negative impacts on ecosystems. The use of microorganisms as biocontrol agents of PPNs can replace chemical control. Bioagents are considered to be both safe and affordable (Mukhtar *et al.,* 2017). Over the last few decades, biocontrol using rhizosphere bioagents (e.g. bacteria and fungi) has been effective in improving plant growth and influencing nematode reproduction via a variety of mechanisms, like producing growth regulators, bioactive compounds, and enzymes that act directly on nematodes (Rocha *et al.*, 2019; Hussain *et al.*, 2020a). Biological control agents (BCA) appear to be a promising tool for controlling phytopathogens. This study aims to review the current threat of rook-knot nematode infection on crops, biological control, antagonistic bioagents, and their mechanisms, and future directions in agriculture to provide a basis for the broad management of root-knot nematodes.

The current threat of root-knot nematode infection on crops

RKNs are among the most significant pathogenic organisms due to their global distribution, capacity for destruction, and economic importance (Khan *et al.,* 2020). Diseases caused by PPNs, cost the global economy over $150 billion annually (Sivasubramaniam *et al.,* 2020; Seong *et al.,* 2021), with RKNs responsible for more than half of these losses (Silva *et al.,* 2021). The quality and quantity of plant production output can be negatively affected by PPNs, pests, and diseases (Holajjer *et al.,* 2020; Perpétuo *et al.,* 2021). RKNs are one of the globe's most devastating nematode groups, causing substantial economic harm to a vast number of arable crops in tropical and subtropical environments *(*Janssen *et al.*, 2016; Karuri *et al*., 2017*)*. RKNs are rhizosphere parasitic nematodes that infest over 5000 species of plants around the world, including a variety of vegetables, commercial crops, shrubs, and trees (Costa *et al.,* 2019). According to a recent study, the top ten parasitic nematode taxa in molecular plant pathology are ranked by scientific and commercial significance (Sánchez Monge *et al.*, 2015). Tomato, carrot, melon, tobacco, kenaf, sugar cane, tea, and coffee are just a few of the over 2000 plant species susceptible to *Meloidogyne* sp., which poses the most economically significant threat to agricultural crop output (Tranier *et al*., 2014; Postnikova *et al.,* 2015). Even though the host range of many RKNs overlaps, not every RKN pathogen may attack the same plants. *Meloidogyne* sp. is widely regarded as the most destructive worm parasite of eggplant (Ye *et al.,* 2019, Yergaliyev *et al.,* 2020). Their infection begins with root penetration by second-stage juveniles (J2), which hatch in the soil from eggs left in egg masses on infected roots by females (Arshad *et al.,* 2021; Bridge and Starr, 2019). Chlorosis (yellowing), rotting, wilting, root galling, early leaf shedding with severely stunted growth, and root development anomalies are all common signs of RKN attack, leading to huge crop losses (Philbrick *et al.,* 2020; Arshad *et al.,* 2021). *M. incognita* and *M. javanica* are two dormant RKN species in Pakistan since they are common in vegetable-growing areas, severely limiting growth and yield (Mukhtar, 2018). Root-knot nematodes are a danger to economic crop farming around the world. Nematode inoculum development and annual production of the same cultivars on the same land are the primary causes of their yield losses (Mukhtar and Hussain, 2019; Mukhtar and Kayani, 2020). Because nematodes can increase susceptibility to other parasites, the severity of this damage can be substantially great (Mabbott, 2018). Crop loss caused by nematodes is estimated to cost between \$80 and 118 billion dollars per year (Roopa and Gadag, 2020). It is estimated that these worms cause 18–20.7% of tomato production losses, accounting for one-third of the losses normally attributed to pests and diseases (Hajihassani *et al.,* 2020). When nematode populations are low, the foliar symptoms may or may not be present. Furthermore, RKN infestation can make the host plant more vulnerable to other diseases, such as root rot and *Fusarium* crown, in areas where these pathogens are present (ColaC Ateş *et al.*, 2018; Abd-Elgawad, 2019). RKNs are difficult to identify and control because they live in infected host plants below the soil surface. *Meloidogyne* sp. has always been difficult to control owing to its high reproductive potential and extensive host specificity, which restricts crop rotation's effectiveness. (Bridge and Starr, 2019; Philbrick *et al.,* 2020). Plant mortality, lower production, decreased chlorophyll content, and a variety of other negative physiology are all additional symptoms and damages of root-knot nematode infestation (El-Sagheer, 2019; Guerrero Abad *et al.*, 2021).

Biological control of root-knot nematodes

To ensure food quality in agricultural production, a variety of plant diseases must be handled and managed well (Sharma *et al.*, 2019). Several approaches and treatment options are used around the world to manage, relieve, and inhibit disease in plants (O'Brien 2017; Singh *et al.,* 2019b). The need for synthetic chemicals in the control of diseases in plants is becoming less popular around the world. Today, many types of research are being done to develop safe, environmentally acceptable, and efficient options to synthesize pesticides for reducing decomposition damage in cultivated crops and managing plant diseases in the field, both of which result in significant economic losses (Droby *et al.,* 2016; Nabi *et al.,* 2017). Biocontrol is a term commonly used in plant pathology and entomology. Biocontrol is used in the field of plant pathology to suppress the buildup of pathogens in the microbial population, whereas biocontrol in entomology is used to suppress the multiplication of parasitic insects against pathogenic microbes, entomophagous nematodes, or predation parasites (Hajek and Eilenberg, 2018; Singh *et al.,* 2020). Biocontrol is also defined as "the employment of microbes or their metabolites to eliminate or reduce pest-related damages or losses" (Barratt *et al.,* 2018; Van Lenteren, 2021). Bioagents, which occupy the same rhizospheric zone as pathogens and absorb the same nutrients, are often used to manage diseased plants (Thakur and Singh, 2018; Hussain *et al.,* 2020a). Biocontrol could be accomplished in a variety of ways, including partial, significant, and entire control. Biological control agents have shown promise as a cost-effective and ecologically friendly pest control approach (Subedi *et al*. 2020; Karimi *et al*., 2021). Several antagonistic organisms, including soil fungi from the genera *Trichoderma* (*Hypocreaceae*), *Verticillium*, *Pochonia*, and *Paecilomyces*, have been tested against *Meloidogyne* sp. and have been commercialized (Anwer 2017; Kiriga 2018). In diverse crops and experimental situations, a variety of fungi, including *Pochonia chlamydosporia* isolates, were tested as RKN bioagents (Escudero *et al*., 2017; Peiris *et al.,* 2020; Tazi *et al.,* 2021). Pathogen growth is suppressed while plant growth and development are promoted by *P. chlamydosporia* colonization of the root (Kumar *et al.,* 2018; Zhuang *et al.,* 2021). *Pochonia chlamydosporia* has been proven to be a bioagent for RKNs and cyst nematodes. This fungus parasitizes RKN eggs within 24 hours, preventing them from hatching by more than 55% (Nagachandrabose, 2018). *Trichoderma* sp enables the development of biocontrol strategies for economically significant plant infections (Guler *et al.,* 2016). *Trichoderma* sp. has an antagonistic effect on *Pythium ultimum* and *Rhizoctonia solani* due to the production of secondary metabolites (Khan *et al.,* 2020). *Purpureocillium lilacinum*, formerly *Paecilomyces lilacinus* (Juyal *et al.*, 2018; Raghavan *et al.,* 2018), is a saprophyte that parasitizes nematode sedentary stages, particularly their eggs, which are generally deposited in a gelatinous matrix, as well as female nematodes (Kiriga, 2018; Walia *et al.,* 2021). Because of its strong potential for biological nematode control, it has been successfully used on tomatoes against *M. javanica* and *M. incognita* (Kiriga *et al.*, 2018; Dahlin *et al.,* 2019). *Bacillus subtilis, Bacillus sphaericus*, and *Pseudomonas fluorescens* are the antagonistic rhizobacteria that affect RKN (Ahmad *et al.,* 2020; Migunova and Sasanelli, 2021). *Agrobacterium, Enterobacter, Aureobacterium, Chryseobacterium, Alcaligenes, Corynebacterium, Klebsiella, Paenibacillus, Phyllobacillus, Xanthomonas, Telluria, and Rhizobium*, are among the other genera mentioned (Rubio *et al.,* 2019). Fungi from the *Trichoderma* and *Purpureocillium* genera (Baron *et al.*, 2020), endospores of *Pasteuria penetrans*, and commercially available rhizobacteria (e.g., *Bacillus firmus*) hold the most promise for biological control of RKNs (*Meloidogyne* sp.) (Engelbrecht, 2019; Abd-Elgawad, 2020). Biological management approaches appear to be less expensive, making them more accessible to farmers and contributing to the agricultural sector's long-term viability. Bioagents are mostly developed to reduce pest populations economically (Bielza *et al*., 2020; Gehlot *et al.,* 2021). The activity and performance of biological control agents are influenced by their surroundings.

Bioagents used in controlling root-knot nematodes

A biological control agent (BCA) is an organism that inhibits a pest or disease. They are microbial antagonists that reduce plant disease and phytopathogens in several ways (Verma *et al*., 2019b; Maurya, 2020). Much information on the variety of methods of BCA in the control of plant diseases has been published over the last few decades (O'Brien, 2017; Rashad and Moussa, 2020). For pest and disease management, BCAs offer an alternative to chemical fertilizers and pesticides. Biotechnological applications, such as gene modification, enable us to enhance the characteristics of such bioagents, allowing them to survive in stressful and nutrient-limited environments, producing more antimicrobial phytochemicals under different temperatures and pH conditions than the existing isolates. Once a BCA has established itself in the rhizosphere, it should be able to colonize and compete for space and nutrients with grown roots (Odelade & Babalola *et al.,* 2019; Poveda *et al.,* 2020). BCA will be unable to compete for food and space if it is unable to develop itself in the rhizosphere and grow along with the treated plant's root system (Khan *et al.,* 2011). BCAs for the management of phytopathogens are often fungal or bacterial isolates obtained from the phyllosphere, endosphere, or rhizosphere, and they serve a vital role in pathogen management. Plant-parasitic nematodes are parasites, predators, or antagonists of fungi, bacteria, protozoans, viruses, turbellarians, enchytraeids, mites, predatory nematodes, collembolans, and tardigrades. The above microbes are being utilized to regulate PPN in some agricultural and horticultural crops as biocontrol agents (Hussain *et al*., 2020b; Tóthné Bogdányi *et al*., 2021). Plant diseases can be combated using microbial biological control agents (MBCAs) such as mycoviruses and bacteriophages. In 2017, 101 MBCAs were certified for disease control in Australia, Brazil, Canada, Europe, Japan, New Zealand, and the United States (Köhl *et al.,* 2019; Ji *et al.,* 2020; Zehra *et al.,* 2021). Bioagents or antagonistic microbes hinder pathogen invasion or pathogen establishment in the host plant. The production of extracellular enzymes by the antagonist, competition for food and habitat among pathogens, and pathogenicity detoxification are all related to the biological management of the disease (Odoh, 2017; Sharma *et al.,* 2019). In a variety of ways, microbial biocontrol agents (MBCAs) prevent plants from disease damage. In the absence of direct antagonistic interaction with the parasites, they may develop or activate enhanced resistance to pathogen infections in plant tissues (Köhl *et al.,* 2019). Competition for nutrients and space is another way to come into contact with viruses (Miller *et al.,* 2019). MBCAs can interact with pathogens actively via hyperparasitism or antibiosis. Hyperparasites attack and destroy fungal pathogen hyphae, spores, and resting structures, as well as bacterial pathogen cells. MBCAs protect agricultural commodities from disease damage in a variety of ways. They compete with pathogens for available space and nutrients in an indirect way (Ons *et al.,* 2020). They interact with pathogen species directly via an antibiosis or hyperparasitism mechanism. The production of antimicrobial compounds that suppress bacteria is another direct-mode strategy (Palyzová *et al.,* 2019; Los *et al.,* 2020; Dann and McLeod, 2021). The compounds emerge as potential plant disease control options. Most BCAs that suppress fungal or bacterial plant diseases and pathogens employ one or more pathways. The production of antibiotics, enzymes, or specific active compounds is referred to as antibiosis, whereas competitive displacement is referred to as competition for food or space (Singh *et al.,* 2020). Microbial pathogen-associated molecular patterns (MAMPs) are resistance-inducing stimuli produced by microorganisms that are identified by pattern recognition receptors (PRRs) (De Lorenzo *et al.,* 2018; Mélida *et al.,* 2020; Zehra et al., 2021). The fact that BCAs are pathogen-specific and unlikely to harm non-target species is the major advantage of using them. Weeds, worms, insects, micro-pathogens, mites, and even vertebrates are among the target species controlled by biocontrol agents. Some phytopathogens are so toxic that they kill the organisms they infect (Singh *et al.,* 2020; Zhang *et al.,* 2020).

Mechanism of antagonistic fungi

Fungal antagonists are now recognized as a rapidly expanding natural phenomenon with a wide range of agricultural applications, including food production and yield. Biological control agents such as antagonistic fungi are used in agriculture. Fungi have a high rate of sexual and asexual reproduction, are target-specific, and have a short generation period, which has increased the potential for biological control agents to combat plant diseases. Most fungal species have defense systems that enable them to effectively defend plants against plant pathogenic fungi-caused diseases. Regardless of the process of fungi seizing or parasitizing, the association of both host-pathogen and fungi or prey entails the infiltration of the outermost body shell. This infiltration subsequently leads to the pathogen's colonizing the body's interior tissues via digestion, enabling it to satisfy its nutrient requirement (Branine *et al.,* 2019; Tawidian *et al.,* 2019). Despite being saprophytes, these fungi can trap nematodes in the soil during their larval or free adult stages. Hydrolytic enzymes found in the cuticle, such as lipases and chitinase, are thought to be responsible for fungi's ability to kill insects and pests (Amobonye *et al.,* 2020; Lin *et al.,* 2021; Litwin *et al*., 2020). Extracellular proteases hydrolyzing the cuticle of worms have been shown to produce peptides that can result in trap formation (Ahmad *et al*., 2021; Liang *et al.,* 2019; Shalaby *et al.,* 2020). RKNs (*M. javanica*, and *M. incognita*) have all been demonstrated to be suppressed by *Paecilomyces lilacinus* and *P. lilacinum* (Iqbal *et al.*, 2018; Tariq *et al.,* 2020; Xu *et al.,* 2021), with good results against Meloidogyne spp. (He *et al.,* 2020). The production of proteases and chitinases by the fungus is linked to the infection process (Xu *et al.,* 2021). The enzymes pierce the eggshell's vitelline layer, allowing mycelium to infiltrate, proliferate, and harm early embryonic developmental stages. The hyphae breach the eggshell and multiply when the egg contents are depleted, parasitizing other eggs in the egg mass (Islam *et al.,* 2021). Chemical compounds and extracts generated by a variety of fungi are important in plant-pathogen biocontrol activities as well (Latz *et al*., 2018; De Silva *et al.,* 2019; Keswani *et al*., 2020). *Trichoderma*, *Paecilomyces* (Al-Hazmia *et al.,* 2019), *Pochonia*, and *Arthrobotrys* (Kassam *et al.,* 2021) are well-known *Meloidogyne* sp. inhibitors. *Pochonia chlamydospores* have been demonstrated to parasitize *Meloidogyne* sp. eggs, and females (Silva *et al.,* 2017; Ghahremani *et al.,* 2019). *Pochonia chlamydospores* are among the most extensively researched biocontrol agents (BCA) against PPNs in the world today (Lubian *et al.,* 2017). *Arthrobotrys* sp. produces hyphae with sticky features that catch and feed on nematodes as a nematophagous fungus (Cao *et al.,* 2018; Karakaş 2020). When used before planting tomato seedlings, *Arthrobotrys dactyloides* reduced the quantity of M. incognita (Peiris *et al.,* 2020; Soliman *et al.,* 2021). *Meloidogyne* sp. is also known to be antagonized by fungi from the genera *Trichoderma* and *Fusarium*. It has been demonstrated that *Trichoderma* sp. can invade plant root surfaces. This has been linked to its ability to minimize root-knot disease (Mukhtar *et al.,* 2021; Wang *et al.,* 2021b) as well as competition with nematodes. *Trichoderma* sp. successfully decreased

Meloidogyne sp., second-stage juvenile (J2) densities, and egg production in tomato roots (Dahlin *et al.,* 2019; Kiriga *et al.,* 2018; Tazi *et al.,* 2021). *Trichoderma* is rhizosphere dwellers that colonize the surface of plant roots. Their antagonism effect is primarily directed at fungi, yet has an impact on the life cycle of the RKN (Rawal, 2020; Sarker *et al.,* 2021). *Trichoderma* sp. aids plant development by inhibiting nematode penetration. *Trichoderma* conidia attach to the cuticle or eggshell of worms and parasitize them (Du *et al.,* 2019; Zhang *et al.,* 2020; Ahmad *et al.,* 2021). Mycoparasitism and entomopathogenicity are the two primary mechanisms by which fungal biological control agents kill agricultural pests and insects. Mycoparasitism is the interaction of a fungus parasite and a fungus host. In contrast, entomopathogenic fungi are parasitic fungi that can kill pathogens. Fungi that control fungal infections in plants via mycoparasitism are known as *Gliocladium* and *Trichoderma* (Vinale *et al.,* 2014; Gomes *et al.,* 2015). Toxic chemicals generated by fungi can affect the pathogens of the host organism (Ramesh and Radhakrishnan, 2020). *Trichoderma* species are known to produce toxins and antibiotics such as viridian, fusaric acid, lilacin, oxalic acid, trichoderin, trichodermol A, harzianolide, and penicillic acid, which suppress the development of RKNs (Devi, & Bora *et al.,* 2018). *Trichoderma* sp. is also being proposed to combat plant diseases and phytopathogens through mycoparasitism, competition, antibiosis, hydrolysis of enzymes, and induced host resistance, among other methods (Silva *et al.,* 2019; Deb and Das, 2020). *Trichoderma* also produces chemicals that harm nematode cuticles, such as volatile organic compounds, 6-pentyl-pyrone, and metabolites (Basit *et al.,* 2021). In addition to direct antagonism, *Trichoderma* sp. manages *Meloidogyne* through a range of methods, including the generation of fungal metabolites (e.g., AAL toxins 3–10, helvolic acid) and induced resistance (Abdelrahman and Jogaiah, 2019; Al-Ani, 2018). Direct antagonism, indirect antagonism, and mixed path antagonism are the three types of intraspecific antagonistic processes related to biocontrol (Ramesh and Radhakrishnan, 2020). Hyperparasitism is a type of predation that underpins direct antagonism. Predation, toxic metabolite formation, and competition for space and nutrients are all examples of direct antagonism. Mixed path antagonism is induced by metabolic enzymes, physical, chemical inference, antibiotics, and uncontrolled byproducts. Indirect antagonism, on the other hand, refers to activities that have no direct effect on the pathogens under attack. Indirect antagonism is characterized by two basic processes: competition and host resistance enhancement. Nutrient scavenging via siderophores, leachate consumption, and niche competition are the main mechanisms at work in the competition. The method includes host resistance induction at the molecular level, as well as phytohormone-associated direct pathogen contact (Solairaj *et al*., 2021). ISR has been linked to phytoalexins, pathogenesis-related proteins, phenolic compounds, reactive oxygen species, and other compounds. These also contribute to the development of numerous physiological obstacles, such as the cuticle and cell plant changes, mostly caused by induced plant action (Aragón *et al.,* 2017; Ziv *et al.*, 2018). These mechanisms are energy-dependent, allowing plants to maintain their defense systems. Defensive priming, in contrast to direct-induced resistance, allows for a powerful and quick response at a minimal energy cost (Chen *et al.,* 2019; Mageroy *et al.,* 2020). Mechanisms of plant defense or reactions are activated by MBCAs depending on plant genotype (Maheshwari *et al.,* 2020; Pandey *et al.,* 2021). Siderophores, biosurfactants, volatile organic compounds (VOCs), antibiotics, pyocyanin, and DAP are all used to induce systemic resistance. The production of signal components by MBCAs triggers defensive mechanisms to respond to infections, which is how they work. The biocontrol mechanism, in other words, is reliant on MBCAs' capacity to adapt to and thrive on the plant (Walia *et al.,* 2021; Zehra *et al*., 2021).

Table 1: Fungi species used as bioagents and their mechanisms against root-knot nematodes

Fungi Strain	**Mechanism**	**Target Pathogen and Host Plant**	**Reference**
Trichoderma spp (eg, T. harzianum, T. viride, T. virens, T. atroviride)	Parasitism, Antibiotic production (eg. trichodermin, trichoviridin, dermadin), ISR and SAR, Secretes lytic enzymes (chitinase, glucanases, and protease), toxic metabolites	*M. incognita*. (Tomato), *M. javanica*, (Tomato), *M. graminicola*, (Rice), *M. arenaria*, (Maize).	(Abd-El-Kareem, Elshahawy, & Abd-Elgawad, 2019; Javeed, Al-Hazmi, & Molan, 2016; Muthulakshmi & Devrajan, 2015; Singh, Rajput, Bisen, Singh, & Singh, 2017)
Pochonia chlamydosporia	Parasitism, Toxin secretion	*M. incognita*, (Tomato), *M. javanica*, (Lettuce), *M. hapla*, (Lettuce)	(Kumar, 2020; Saxena, 2018; Tian *et al.,* 2014)
Paecilomyces	Parasitism, Antibiotics (leucinostatin, lilacin),	*M. javanica*, (Pigeonpea), *M.*	(Moosavi & Zare, 2020; Najafi *et al.,*

lilacinus	Enzymes (chitinase and protease).	*incognita*, (Tomato) *M. arenaria*, (Brinjal)	2016; Senthilkumar, Anandham, & Krishnamoorthy, 2020; Umamaheswari *et al.*, 2020)
Aspergillus niger	Parasitism, Induces systemic resistance (ISR)	*M. incognita*, (Mung bean), *M. javanica*, (Pigeonpea), *M. arenaria*, (Tomato).	(Al-Ani, 2018; Jin *et al.*, 2019; Khanna *et al.*, 2021; Nam, Anderson, & Kim, 2018; Yeon *et al.*, 2021)
Verticillium chlamydosporium	parasitism	*M. incognita*, *M. javanica* and *M. arenaria* (maize, kale and Phaseolus).	(dos Santos, Esteves, Kerry, & Abrantes, 2013; Giné, Carrasquilla, Martínez-Alonso, Gaju, & Sorribas, 2016; Tranier *et al.*, 2014)
Arbuscular mycorrhizal fungi (AMF)	Parasitism	*M. incognita* (sweet, pepper, tomato)	(Herrera-Parra, Ramos-Zapata, Basto-Pool, & Cristóbal-Alejo, 2021; Vos *et al.*, 2012)
Syncephalastrum racemosum	Secondary metabolites, production of toxins, enzymes, ISR, and parasitism	*M. incognita* (Cucumber)	(Huang *et al.*, 2014)

Mechanism of antagonistic bacteria

Several bacterial strains have been shown to have the potential to become biocontrol agents. *Bacillus*, *Pseudomonas*, and *Azotobacter* isolates from plant roots displayed antagonistic activity against the plant pathogen and acted as disease control agents (Verma *et al.*, 2019a; Migunova and Sasanelli, 2021). The bacterial group which colonizes and supports the development of plants' roots is known as plant growth-promoting rhizobacteria (PGPR) (Noumavo *et al.*, 2016; Qiao *et al.*, 2017). The above (PGPR) are among the most efficient and sustainable BCAs for controlling plant pathogens and disease (Shaikh and Sayyed 2015; Vejan *et al.*, 2016). Because

PGPR is non-toxic, naturally occurring microorganisms with long-term use, they have many advantages over chemical biocontrol agents. *Pseudomonas* sp. and *Bacillus* sp. have been regarded as significant bioagents in the fight against root and soil-borne diseases in a variety of crops, including wheat, tomato, potato, and chickpea (Nguvo *et al.,* 2019; Hussain *et al.,* 2020b). Antimicrobial metabolites generated by bacteria bioagents of the genera *Agrobacterium*, *Bacillus*, *Pantoea*, *Pseudomonas*, *Serratia*, *Stenotrophomonas*, *Streptomyces*, and others have been identified, with a majority of them having broad-spectrum action. *Bacillus* has been studied for lipopeptides like iturin, surfactin, and fengycin, whereas *Pseudomonas* has been studied for antibiotic metabolites like DAPG, pyrrolnitrin, and phenazine (Kenawy *et al.*, 2019; Dimkić *et al.*, 2022). Many antibiotics are only made after a bacteria reaches a certain level of resistance. In phenazine-producing *Pseudomonas*, this quorum-sensing mechanism is well understood. Plant growth secreted toxin surface chemicals (bio-surfactants) and volatiles, chitinase cell wall-degrading enzymes, and -1,3-glucanase enhancing rhizobacteria to reduce soil-borne pathogens (Youssef *et al.,* 2018; Sayyed *et al.,* 2019; Wang *et al.,* 2021a). The release of siderophore ligands, which efficiently grab iron and inhibit pathogen development, was previously identified as a biocontrol mechanism (Parray *et al.,* 2019; Avelar, 2021).

Table 2: Mechanism of bacteria bio-control agents in controlling root-knot nematodes

Bacteria Strain	**Mechanism**	**Target Nematode**	**Reference**
Pasteuria penetrans1	Predation	*Meloidogyne spp.*	(Subedi, Gattoni, Liu, Lawrence, & Park, 2020)
Pseudomonas spp. (P. aeruginosa, P. stutzeri, P. fluorescens, P. putida)	Hydrogen cyanide (HCN), Diacetylphloroglucinol (DAPG), ISR and SAR, Pyoluteorin, Extracellular protease	*M. incognita, M. javanica*	(Avelar, 2021; Khanna *et al.*, 2021)
Serratia marcescens	Volatile metabolites, Prodigiosin	*M. incognita, M. javanica,*	(El-Ashry, Ali, Awad, & Control, 2020; Zhao *et al.,* 2021)
Bacillus spp. (e.g B. cereus, B. coagulans B. megaterium, B.	Antibiotic production, Hydrolytic enzymes (Chitinase, Protease,	*M. incognita, M. javanica, M. graminicola, M.*	(Ahmad, Khan, Khan, Ali, & Mohhamad, 2021;

licheniformis, B firmus)	Sphingosine), ISR, Secondary metabolites,	*arenaria*	Subedi *et al.,* 2020)
Corynebacterium paurometabolum	Hydrogen sulfide, Chitinase	*M. incognita*	(Márquez *et al.,* 2019; Subedi *et al.,* 2020)
Rhizobium etli	ISR	*M. javanica* (Tomato)	(Topalović & Heuer, 2019; Xia *et al.,* 2019)

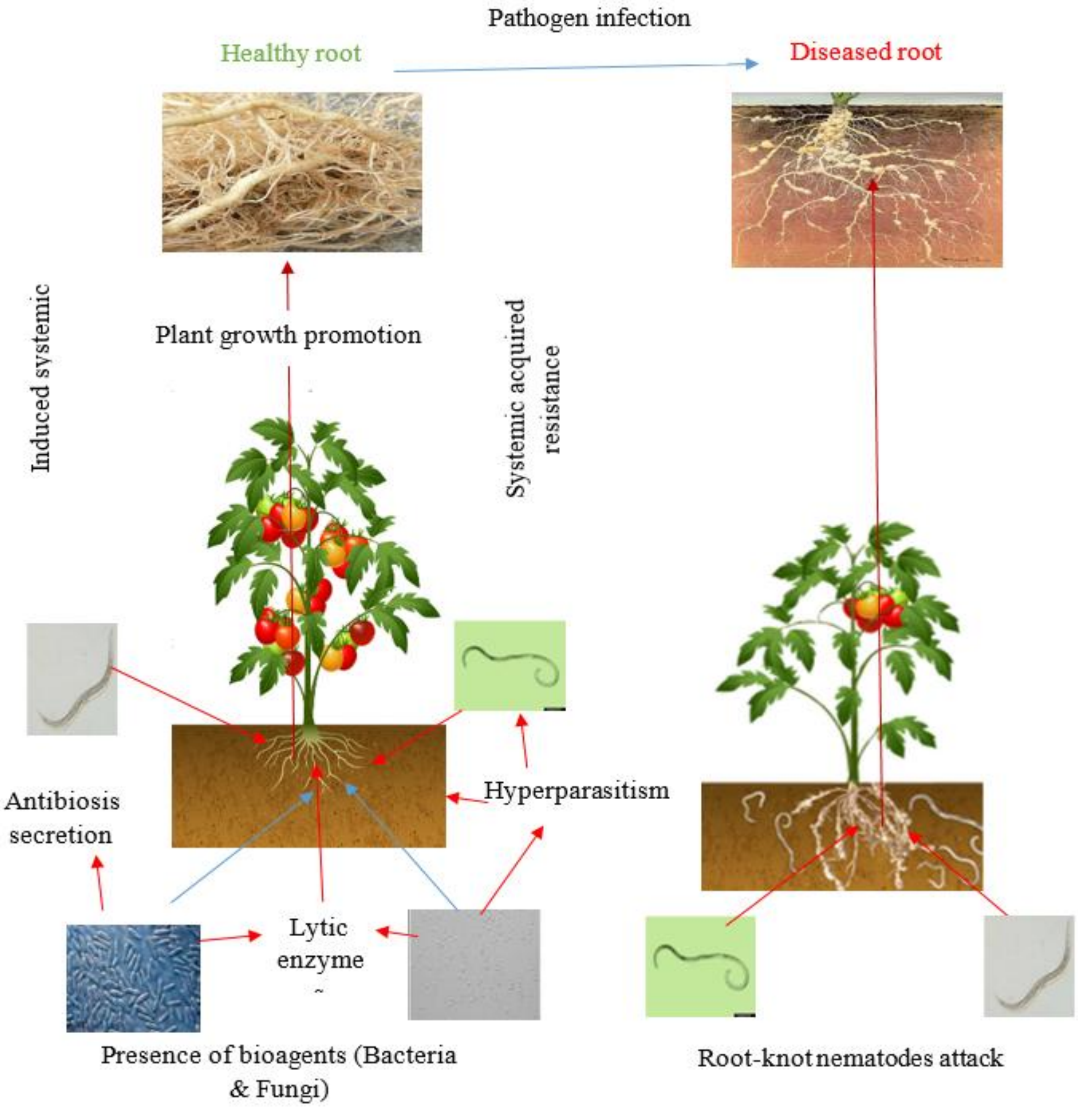

Figure 1: Mechanism of Antagonistic Bioagents (Bacteria & Fungi) in Controlling of Root-Knot Nematodes

Future direction / prospects

Man has worked since ancient times to improve agricultural productivity and reduce disease susceptibility in crops by adopting agricultural methods that minimize both diseases and pathogens (Thurston, 2019; Thambugala *et al.,* 2020). Food security is a top priority for all governments, but it is especially important in developing countries with rapidly growing populations (Emami *et al.,* 2018). Food crop production must be expanded to satisfy the nutritional demands of a growing population. Overuse of synthetic pesticides, on the other hand, is an unsustainable practice that comes at a high cost in terms of environmental harm and organism health. Commercial uses and implementations of plant disease biocontrol have been delayed due to the variable effectiveness of BCAs in different climatic environmental conditions as well as host specificity. Recent advancements in science have enabled us to learn more about molecular action mechanisms like the production of nemato-toxins, signaling pathways that activate the host-plant defense mechanisms, and the infestation process. This knowledge must lead to the development of new approaches to enhance the effectiveness of BCAs for biocontrol implementations against RKN, increasing the microbial secretion of toxic compounds or metabolites, and developing commercial nematicidal agents. To overcome this challenge, new biotechnological techniques must be developed to generate BCA formulations with greater stability, efficiency, and survival to overcome this challenge (Legrand *et al*., 2017; Adeniji and Babalola, 2018). BACs are expensive to commercialize because they require several steps, including microorganism isolation in pure culture or enhancement, identification, and characterization, formulation development, mass production, product efficacy testing, storage durability inspection, finding a manufacturing partner, licensing and marketing, health, and ecological safety considerations (Backer *et al.,* 2018; Bubici *et al.,* 2019; Soumare *et al.,* 2020). Agriculture's biodiversity is essential for its long-term existence. Effective biocontrol agents produce economic advantages, and their contribution to the management of preexisting pest species, predators, and pathogens has been investigated (Barratt *et al.*, 2018; Lacey *et al.,* 2015). There is a majority of research in this sector being done in the lab, and there has been minimal focus on generating practical bioagents in the field. Furthermore, because of a lack of understanding about their application, cost-effective products are not widely explored by growers. Therefore, efforts must be made to popularise biological control. When deployed in the field, BCAs that appear promising in the lab frequently fail. Biotechnology and other molecular approaches have recently gained attention as prospective solutions to the problem of improving BCA selection and characterization. To improve the efficacy of BCA for viable marketability, complete knowledge of BCA mechanisms, and environmental evaluation, various strategies such as mutation or protoplast fusion should be applied. The bulk of bioagents does poorly in field testing yet excel in the laboratory. However, there are various reasons for this, the majority of which can be linked to environmental and physical obstacles that hinder metabolic efficiency. Compounds synthesized by bioagents are important to today's agricultural production environment. However, their utilization must be fully studied. The majority of research in this area is currently done in the lab, with minimal emphasis on generating profitable bioagent formulations. To maximize the efficiency of these agents, new application procedures must be developed. Furthermore, due to a lack of awareness of how to use cost-effective items, farmers have found it difficult to do so. As a result, a more fundamental study in this field is needed to develop the concept of biological control extension.

Conclusion

Considerably, much research has been conducted over the last two decades to probe the use of microbes as biocontrol agents antagonistic to nematode pests. Many BCAs have been recognized as plant-parasitic nematode pathogens and have been shown to suppress nematode pest infestations. However, just a few economically viable biological control products derived from BCAs with nematicidal potential have been established and used in agriculture. Researchers have reported on a variety of bio-agents for root-knot nematode treatment, including fungi and bacteria. The efficacy of the bioagent differed depending on whether it was evaluated in vitro or the field. This could be due to inconsistencies between the in vitro and field conditions. In vitro and the field, bioagents such as *Verticillium*, *Pochonia*, *Paecilomyces*, *Trichoderma* sp., *Pseudomonas* sp., *Agrobacterium*, and *Bacillus* sp. showed considerable suppression of root-knot nematode infestation. These bioagents must be used in a wider range of applications. In addition, emerging bioagents with broader applications must be thoroughly explored to better understand and apply them. Antibiotics, siderophores, cell wall disintegrating enzymes, volatile organic compounds, mycoparasitism, competition for space, and nutrients are all documented processes of bioagents in the reduction of root-knot nematodes, as is resistance induction. To achieve optimum biocontrol effects in practice, regardless of how friendly and economic nematode antagonist is to a specific host in a lab experiment, an intensive investigation of the antagonist's mechanisms against nematode populations, as well as a deep understanding of the relationships between biological control strains, nematode targets, microbial biomass, plants, and the ecosystems, should be conducted. Finding new and biocontrol microorganisms that are highly effective against phytopathogens is also very significant. Finally, bioagents should be used for specific diseases and pathogens, as well as in the fields where they have the most promises.

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