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REVIEW

# Interactions between entomopathogenic nematodes and entomopathogenic fungi in the aspect of new possibilities for biological plant protection

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**Abstract**

Entomopathogenic fungi (EPF) and entomopathogenic nematodes (EPNs) have a strategic and important role in the biological control of agrophages. Micro- and macro-organisms have become an alternative to chemical methods, not only reducing the use of chemical pesticides, but also preventing agrophages from becoming resistant to chemicals and minimizing risks to human, animal and environmental health. The common habitat of EPNs and EPF is the soil, but interactions between them have mainly been studied in the laboratory. Recently, there has been a growing interest in combining biological control agents to increase their efficacy, and many studies have focused on combining EPF and EPNs against different insect pests. Studies have shown synergistic, additive or antagonistic effects. The results of these interactions depend on the pathogen, the host species, the different times of infection and the choice of the appropriate pathogen dose. The aim of this review was to summarize the existing knowledge on the life cycle of nematodes and the mechanisms of action of EPF and their application in practice, as well as the interaction between EPNs and EPF in plant protection against insect pests.

**Keywords**: biological control, entomopathogens, fungi, interactions, nematodes

## Introduction

Intense environmental changes in recent years are posing a major challenge to modern agriculture. A warming climate, lower availability of fresh water, and emerging armed-political conflicts resulting in declining cultivated areas are becoming a problem. In addition, intensive agricultural production contributes to the degradation of arable land by reducing organic matter, nutrients, and biodiversity (Gullino *et al*. 2021). Large-scale farming makes it easier for diseases and pests to spread, and the high degree of chemicalization of agriculture is creating pesticide-resistant organisms and exacerbating food safety concerns (Premanandh 2011; Savary *et al*. 2019). Gaugler and Kaya (1990) showed that applied insecticides can enter the food chain and have long-term effects on organisms, including humans. Since chemical pesticides pose a risk to human health and the environment, new options for crop protection need to be found. Alternatives to chemicals are biopesticides, which are based on the use of living organisms, i.e., micro-organisms (bacteria and fungi), viruses or macro-organisms (parasitic nematodes, predatory mites, and parasitic and predatory insects). These organisms can be introduced into the environment by an augmentative method, involving the introduction of a large number of beneficial micro- or macro-organisms that are naturally occurring enemies of pests (Collier and Van Steenwyk 2004). Organic food production is becoming increasingly popular in Europe, including Poland, and the area under organic crops is gradually increasing.

Biopreparations, including those containing EPNs or EPF, are gaining acceptance in plant protection (Kruk and Dzięgielewska 2019; Sharapova 2019). Fungi and nematodes belong to a group of biotic agents that play several important roles in the environment and influence human life and activities. The biodiversity of microorganisms present influences the balance of individual environments. These include fungi and nematodes that parasitize other organisms and act as natural bioregulators in the environment. EPNs include the genera *Oscheius*, *Steinernema* and *Heterorhabditis* (Torrini *et al.* 2015; Poinar 2018). Their juveniles in the infective juvenile larva (IJs) stage live in the soil and are responsible for actively seeking out the host insect. Furthermore, IJs can survive at temperatures between 5°C and 35°C without losing their pathogenicity. EPNs are associated with bacteria, that once released into the insect's body, cause death within 24-48 hours (Gaugler 2002). Equally important bio-regulators of plant pests are EPF, which infect insects mainly in the soil environment. The most common EPF in the environment are *Entomophtora*, while biopesticides belonging to the genera *Beauveria, Cordyceps* (*Isaria*) and *Metarhizium* are most frequently used. Due to the wide range of infected hosts, EPF are found in aquatic and soil environments in all climatic zones. The wide range of occurrence has led to the development of a significant biodiversity (Araújo and Hughes 2016). The process of infecting prey involves the fungal spore entering the insect's body surface, germinating, and growing through the epidermis or chitinous exoskeleton. Under conditions of optimal humidity and temperature, the fungal hyphae completely colonize the insect's body. Depending on their morphology, the fungi form yeast-like threads, protoplasts, or filaments inside the host (Araújo and Hughes 2016). Most EPF kill their host before they can produce spores. The entire infection process takes about 4–7 days (Litwin *et al*. 2020; Quesada-Moraga *et al*. 2020). The combined use of EPF fungi and EPNs could be an innovative approach to pest control. Research to date has mainly been based on laboratory studies and have primarily focused on the insecticidal efficacy of fungi and nematodes, while their interactions and possible effects under natural conditions are largely unknown. Most research has reported an additive effect of the combination of EPNs and EPF on the mortality of some insect species, but in some cases an antagonistic interaction was found (Barbercheck and Kaya 1991; Ansari *et al*. 2004; Shapiro-Ilan *et al*. 2004; Tarasco *et al*. 2011; Půža and Tarasco 2023). Due to the different defense mechanisms of the pest, it is necessary to try to combine the use of EPF and EPNs. The entomopathogenic activity of these organisms is based on different actions, so the likelihood of an insect developing defense mechanisms against several pathogenicity mechanisms at the same time is very low (Spescha *et al*. 2023). The development of EPF and EPNs resistance is therefore unlikely to pose an environmental risk in the future.

## Mechanisms of action of entomopathogenic fungi and their use in practice

Entomopathogenic fungi are a special group of soil-dwelling microorganisms that infects and kills insects through cuticle penetration (Pell *et al*. 2010). Fungi have an important role as reductants, contributing to the decomposition of organic compounds and promoting the cycling of elements in the environment (Gadd 2007). A significant proportion of fungi cause plant diseases. Pathogens can weaken and damage crops, causing economic losses in agriculture and food production (Thambugala *et al*. 2020). The polyphagous nature of some fungal species affects their rapid spread and makes effective control difficult. Environmentally relevant parasitic fungal species are used for biological control (Singkaravanit *et al*. 2010). EPF are found in the Ascomycota, Zygomycota, Deuteromycota, Chytridiomycota and Oomycota clusters. The life cycle varies from group to group but is primarily based on infecting the host and causing death (Kidanu and Hagos 2020). All EPF are transmitted by spores (Araújo and Hughes 2016). The infection process begins with the attachment of the spores to the insect's epidermis, facilitated by the appressorium. This is the filamentous structure responsible for attaching the germinating spore to the surface of the host's epidermis. Penetration of the epidermis and growth of fungal hyphae inside the prey's body follows, along with secretion of lipases, proteins and chitinases. Insects may respond to the presence of entomopathogenic fungi in their bodies through several physiological mechanisms, e.g., immune and antioxidant responses (Aghaeepour *et al.* 2023). The host dies as a result of mechanical damage caused by the proliferating hyphae and by poisoning with toxins produced by the pathogen (Kidanu and Hagos 2020). Secondary metabolites produced during infection, including destruxins and cytochalasins, may be directly involved in killing the host or suppressing its defense responses, thereby indirectly aiding the pathogen (Fig. 1) (Vilcinskas *et al*. 1997).

A common phenomenon among fungi is antagonism – the substances they produce reduce the growth of other microorganisms, including fungi. There are known cases of antagonistic effects of entomopathogenic fungi on pathogenic fungi such as *Rhizoctonia*

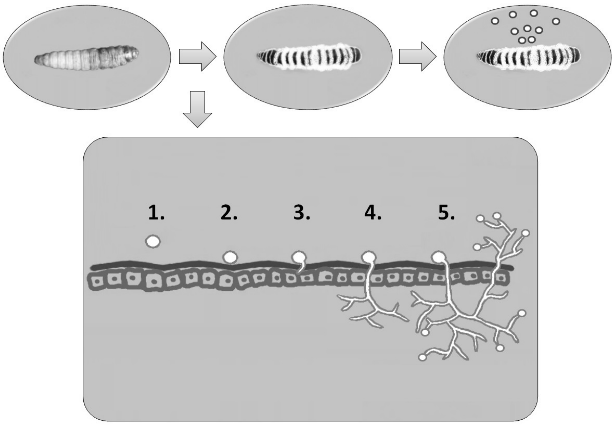


**Fig. 1.** Life cycle of entomopathogenic fungi: 1 – infective stage – spore, 2 – spore adhesion to the epidermis, 3 – spore germination, 4 – growth of fungal hyphae inside the host body, 5 – death of the host and appearance of the outside mycelium with spores

*solani* Kühn and *Pythium myriotylum* Drechsler (Ownley *et al*. 2008). Some mycotoxins may have nematicidal activity. Beauvericin, secreted by fungi of the species *Beauveria bassiana* (Bals. – Criv.) Vuill. and *Beauveria pseudobassiana* (S.A. Rehner and Humber), has been shown to significantly reduce the incidence of the pine wood nematode (*Bursaphelenchus xylophilus* Steiner and Buhrer), with up to 100% nematicidal efficacy in some variants (Sánchez-Gómez *et al*. 2023). Insect-pathogenic fungi play an important role in reducing plant pests. In the environment, aphid epizootics caused by fungi of the order Entomophthorales are frequently observed (Bałazy *et al*. 2008). Unfortunately, this species has no use in biopesticides. In practice, EPF are mainly used to control pests in cover crops, where the conditions are most favorable for their development (Ekbom 1979). For example, high pathogenicity of *B. bassiana* was observed against mealworms (*Tenebrio molitor* L.) and brown marmorated sting bug (*Halyomorpha halys* Stål). Within 10 days of application, 100% insect mortality was achieved under laboratory conditions (Swathy *et al*. 2024). Dannon *et al.* (2020) in their laboratory and greenhouse studies showed a significant effect of *B. bassiana* application on western flower thrips, *Frankliniella occidentalis* (Pergande), with a result of 69–96% insect mortality. Kuźniar *et al.* (2014) showed a positive effect of using *Isaria fumosorosea* (Wize) in faba bean (*Vicia faba* L.) cultivation, where the fungus significantly reduced the damage caused by the feeding of the pea leaf weevil (*Sitona lineatus* L.) on plant roots. In recent years, there has been a significant increase in the use of EPF in field crops, linked to the use of integrated pest management and an increasing range of biopreparations containing different strains of insect-pathogenic fungi (Kidanu and Hagos 2020).

## The life cycle of entomopathogenic nematodes and their use in practice

For commercial pest control, nematodes belonging to the genera *Steinernema* and *Heterorhabditis* are used because of their wide host range, short developmental cycle, and ease of mass production *in vitro*. (Askary and Abd-Elgawad 2017). The life cycle of insect nematodes consists of the following stages: egg, four larval stages and adult. Species belonging to the genus *Steinernema* are dioecious, while in the genus *Heterorhabditis* the first generation is hermaphroditic and subsequent generations are dioecious. The stage that occurs in the soil is the infective juvenile larva (IJ) stage. This stage has the ability to actively seek out the host insect. These larvae enter the insect's body cavity through natural openings, i.e., mouth, anus or fistulae, and, in the case of species of the genus *Heterorhabditis*, by direct penetration of the insect's soft cuticle. After entering the insect host, they reach the haemocoel and release symbiotic bacteria from the gut. Nematodes of the *Steinernema* genus contain bacteria of the genus *Xenorhabdus*, while *Heterorhabditis* nematodes contain bacteria of the genus *Photorhabdus*. These bacteria release toxic and immunosuppressive compounds that kill the insect (Koppenhöfer and Gaugler 2009; Liao *et al*. 2017). When the insect dies, its body is bioconverted into a nutrient medium that helps the nematode grow and reproduce (Fig. 2). During this stage, the bacteria secrete small molecule antibiotics

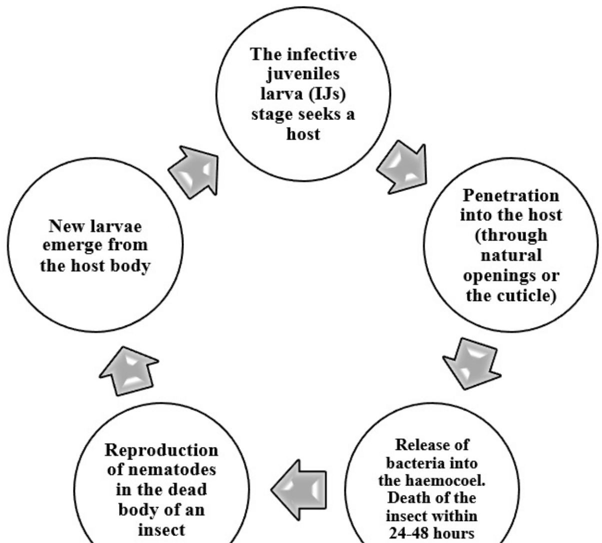


**Fig. 2.** Life cycle of entomopathogenic nematodes of the genera *Steinernema* and *Heterorhabditis*

that protect the dead insect from other bacteria Nematodes, together with symbiotic bacteria, are able to suppress the insect's immune system and weaken the antimicrobial response, e.g., lysozyme and cecropin are inhibited by *Xenorhabdus* species (Park *et al*. 2007; Lalitha *et al*. 2018). Characteristically, insects infected with nematodes of the genus *Heterorhabditis* turn a reddish maroon color. EPNs and their mutualistic bacteria are used commercially as a safe alternative to chemical insecticides. EPNs such as: *Steinernema carpocapsae* (Weiser)*, Steinernema feltiae* (Filipjev)*, Steinernema kraussei* (Steiner)*, Steinernema glaseri* (Steiner)*, Steinernema riobrave* (Cabanillas, Poinar and Raulston)*, Heterorhabditis bacteriophora* (Poinar) and *Heterorhabditis megidis* (Poinar, Jackson and Klein) are among the species that are most often produced on an industrial scale. Through liquid culture, this has low production costs, for example, *H. bacteriophora* and *H. megidis* are successfully used against the black vine weevil (*Otiorhynchus sulcatus* Fabricius), which is considered a dangerous pest of yew, rhododendron, and many other nursery plants (Ehlers 2007). In the case of nematodes of the genus *Steinernema*, the genus *S. glaseri* for grubs, *S. kraussei* for the spruce web-spinning sawfly and *S. carpocapsae* for the *Hylobius* root weevils have been successfully recognized on the market (Shapiro-Ilan *et al*. 2020). EPNs are an effective and environmentally friendly pest control tool. Their versatility, ability to integrate with other crop protection methods (e.g., the use of pheromone traps, light traps or other biological control agents) and environmental benefits make them a valuable component of sustainable agriculture and crop protection programs (Oliveira-Hofman *et al*. 2019).

## Interactions between entomopathogenic nematodes and entomopathogenic fungi

Biopesticides allow the combined use of a wide variety of pathogenic organisms. In recent years there has been increased interest in this mode of action, particularly in the combination of EPF strains with numerous species of EPNs against a wide range of insect pests. The effect of the combined use of entomopathogens can be antagonistic, where the presence of one pathogen inhibits the activity of other organisms, or synergistic, where one pathogen facilitates the infection of other organisms (Fig. 3) (Correa-Cuadros *et al*. 2016; Wakil *et al*. 2017). Most of the studies conducted on the combined use of EPF and EPN have been based on the control of beetles of the families Scarabaeidae and Curculionidae (Coleoptera) and insects of the order Lepidoptera (Shapiro-Ilan *et al*. 2004;

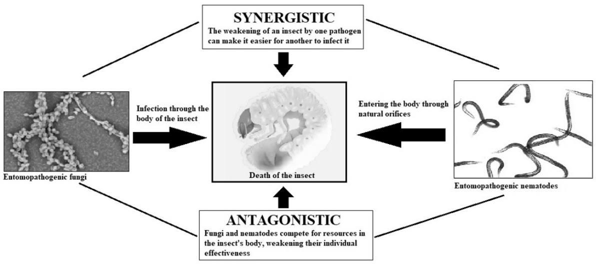


**Fig. 3.** Schematic of the interaction between entomopathogenic fungi and entomopathogenic nematodes

Otsuki and Yano 2014). One example is research into the combination of the fungi *B. bassiana* and *Metarhizium anisopliae* (Metchnikoff) with the nematode *H. bacteriophora* against the larvae of the palm weevil (*Rhynchophorus ferrugineus* Olivier). Additive and synergistic interactions were found in these studies. It was also found that a 1–2-week delay in nematode application after the fungus increased the efficacy of the treatment, as the longer the larvae are exposed to the fungus, the more weakened they become and consequently more susceptible to EPNs (Wakil *et al*. 2017). In the case of insects of the order Lepidoptera, a combination of *B. bassiana* and *H. bacteriophora* was used resulting in an additive effect, causing a higher mortality rate of beet armyworm larvae (*Spodoptera exigua* Hübner). To achieve this effect, a double infestation of nematodes and a fungus was carried out (Barbercheck and Kaya 1991). Ansari *et al*. (2006) observed in field experiments on white grubs (*Hoplia philanthus* Fuessly, Coleoptera: Scarabaeidae) that the combined application of *M. anisopliae* and *H. megidis* resulted in additive or synergistic effects. More than 95% of larval mortality was observed following nematode application 4 weeks after fungal application. Similar additive effects of *Heterorhabditis indica* (Poinar, Karunakar and David) and *M. anisopliae* were shown by Shapiro-Ilan *et al.* (2004) in experiments on pecan weevil larvae (*Curculio caryae* Grub, Coleoptera: Curculionidae). When the fungus *B. bassiana* was used together with *H. indica*, the interactions were antagonistic, as in the variant using *S. carpocapsae* and *Paecilomeces fumosoroseus* (*I. fumosorosea*) Wize.

Studies on EPF and EPNs show that the efficacy of entomophagy depends on a number of abiotic factors. It has been observed that the optimum temperature for spore germination of entomopathogenic fungi depends on the region of origin of the strain and its species, but 20-30°C is considered a favorable temperature range (Gul *et al.* 2014). An important element in the case of fungi is adequate ambient humidity. The most favorable conditions are those where the relative humidity is close to saturation (>95.5%) and this is the range in which the highest level of spore germination is achieved (Abdul Qayyum *et al*. 2021). In the case of EPNs, a broader spectrum of action is shown. Some studies report that lower soil moisture can negatively affect nematode pathogenicity. Maintaining adequate moisture conditions allows the nematodes to move more efficiently and increases their survival rate (Toth *et al*. 2022). The rate of growth and development of EPNs and EPF depends on the substrate in which they occur. Studies by Bueno-Pallero *et al*. (2018) show that

**Table 1.** Interactions between entomopathogenic fungi and entomopathogenic nematodes during application to agricultural pests (Půža and Tarasco 2023)

| Target Pest | Nematode | Fungus | Interaction |
|---|---|---|---|
| *Bactrocera dorsalis*<br>(Diptera: Tephritidae) | *H. bacteriophora*<br>*S. carpocapsae* | *B. bassiana*<br>*M. anisopliae* | additive, synergistic |
| *Bactrocera zonata*<br>(Diptera: Tephritidae) | *H. bacteriophora*<br>*S. carpocapsae* | *B. bassiana*<br>*M. anisopliae* | additive, synergistic |
| *Coptognathus curtipennis*<br>(Coleoptera: Scarabaeidae) | *H. bacteriophora*<br>*S. yirgalemense*. | *M. anisopliae* | additive, synergistic |
| *Curculio caryae*<br>(Coleoptera: Curculionidae) | *H. indica*<br>*S. carpocapsae* | *B. bassiana*<br>*M. anisopliae*<br>*C. fumosorosea* | antagonistic, additive |
| *Curculio nucum*<br>(Coleoptera: Curculionidae) | *H. bacteriophora*<br>*S. carpocapsae*<br>*S. feltiae* | *M. anisopliae* | additive |
| *Cyclocephala lurida*<br>(Coleoptera: Scarabaeidae) | *H. bacteriophora*<br>*H. megidis* | *B. bassiana*<br>*M. anisopliae* | additive, synergistic |
| *Diatraea saccharalis*<br>(Lepidoptera: Pyralidae) | *H. bacteriophora* | *M. anisopliae* | additive, antagonistic |
| *Ectinohoplia rufipes*<br>(Coleoptera: Scarabaeidae) | *H. bacteriophora*<br>*S. carpocapsae* | *B. brongniartii* | additive |
| *Exomala orientalis*<br>(Coleoptera: Scarabaeidae) | *H. bacteriophora*<br>*S. carpocapsae* | *B. brongniartii* | additive |
| *Hoplia philanthus*<br>(Coleoptera: Scarabaeidae) | *H. bacteriophora*<br>*H. megidis*<br>*S. glaseri* | *M. anisopliae* | additive, synergistic |
| *Hylobius abietis*<br>(Coleoptera: Curculionidae) | *S. carpocapsae*<br>*H. downesi* | *B. bassiana*<br>*M. anisopliae*<br>*M. brunneum*<br>*B. caledonica* | additive |
| *Leptinotarsa decemlineata*<br>(Coleoptera: Chrysomelidae) | *S. feltiae*<br>*H. bacteriophora* | *B. bassiana*<br>*C. fumosorosea* | additive |
| *Otiorhynchus sulcatus*<br>(Coleoptera: Curculionidae) | *H. bacteriophora*<br>*S. carpocapsae*<br>*S. kraussei* | *M. anisopliae* | additive, synergistic |
| *Plutella xyllostella*<br>(Lepidoptera: Plutellidae) | *H. bacteriophora* | *B. bassiana*<br>*M. anisopliae* | antagonistic, additive, synergistic |
| *Rhagoletis pomonella*<br>(Diptera: Tephritidae) | *S. carpocapsae*<br>*S. riobrave* | *B. bassiana*<br>*M. brunneum*<br>*C. javanica*<br>*C. fumosorosea* | additive |
| *Rhynchophorus ferrugineus*<br>(Coleoptera: Curculionidae) | *H. bacteriophora* | *B. bassiana*<br>*M. anisopliae* | additive, synergistic |
| *Spodoptera exigua*<br>(Lepidoptera: Noctiudae) | *H. bacteriophora*<br>*S. carpocapsae* | *B. bassiana* | additive |
| *Spodoptera littoralis*<br>(Lepidoptera: Noctuidae) | *H. bacteriophora*<br>*S. riobrave* | *B. bassiana* | synergistic |
| *Thaumatotibia leucotreta*<br>(Lepidoptera: Tortricidae) | *S. jeffreyense*<br>*S. yirgalemense* | *M. pinghaense* | antagonistic, additive, synergistic |
| *Thrips tabaci*<br>(Thysanoptera: Thripidae) | *H. bacteriophora*<br>*S. feltiae* | *B. bassiana*<br>*M. anisopliae* | additive |

the growth effect on a limiting substrate (CMA ¼) is slower than on a rich substrate (PDA), indicating that the availability of resources in the soil plays an important role in the growth and development of EPNs and the growth of EPF. Several biotic and abiotic factors also determine the epizootic capacity of EPF (Mudgal *et al.* 2013). Among the biotic factors, the nematode strain, the density of invasive intestinal nematodes, nematode strain, density of invading IJs, insect host species and insect host age and nutritional status of the host insects have a significant impact on the interaction between EPNs and EPF, as they are linked to the persistence and development of nematode populations and thus influence the infectivity of EPNs (Shaurub 2023).

Secondary metabolites from *Xenorhabdus* and *Photorhabdus* (these bacteria are found in the gastrointestinal tract of nematodes of the genera *Steinernema* and *Heterorhabitis*) have been shown to be effective in competition between EPF and EPNs. For example, Tarasco *et al.* (2011) showed that secondary metabolites produced by *X. bovienii* inhibited the growth of B. bassiana. This is one of the main problems with using fungi and nematodes at the same time. Once inside the insect, EPN and EPF can release specific metabolites to protect the insect from other macro-organisms. With such strong competition in the insect haemocoel, exclusion of one of the organisms may occur (Strasser *et al*. 2000). In contrast, Ansari *et al.* (2008) used a combination of EPF *M. anisopliae* together with EPN – *H. bacteriophora*, *S. feltiae* and *S. kraussei*, which resulted in increased efficacy against black vine weevil (*Otiorhynchus sulcatus*). The application of EPN 1 or 2 weeks after fungus application resulted in 100% larval mortality, even when biological control agents were applied at reduced doses. Another positive effect of the combined application of EPF and EPN was shown by Usman *et al.* (2020). In experiments with *Rhagoletis pomonella* (Walsh, Diptera: Tephritidae), the combination of nematodes and fungi was shown to be more effective than either fungi or nematodes alone.

Current studies on the combined use of EPNs and EPF include seven fungal and 10 nematode species. The studies clearly show a significant effect of bioagents on the efficacy of their combined use (Table 1). Some studies have reported an antagonistic effect of pathogen combinations on application efficacy, but some combinations may have a negative effect on the propagation of both pathogens. Therefore, this aspect should play a key role when considering specific nematode-fungus combinations (Půža and Tarasco 2023).

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