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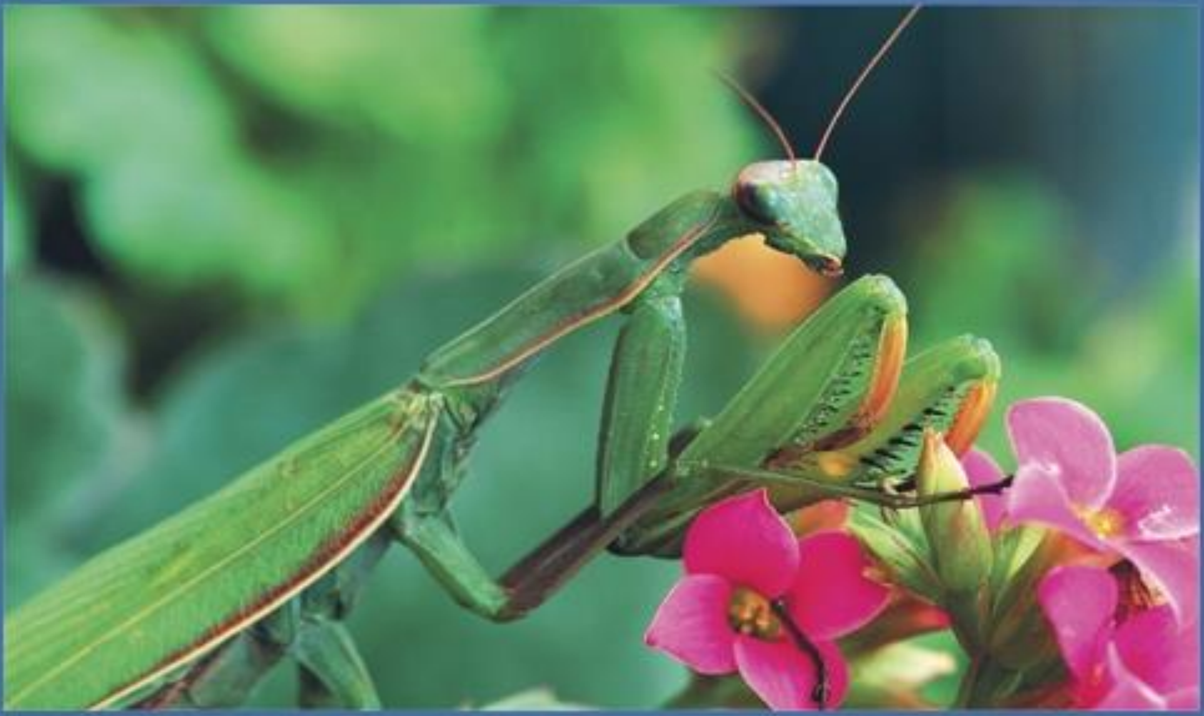

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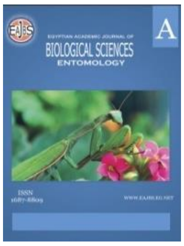

Compatibility of Entomopathogenic Nematodes with Agrochemicals and Biocontrol Potential of their Combinations against Insect Pests: An Updated Review

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ABSTRACT

Entomopathogenic nematodes (EPNs) are biocontrol agents against various insect pests in the world for their characteristics of infectivity and compatibility with different control agents. Several environmental factors directly affect the EPN populations in the soil, as well as the resistance of certain insect pests to EPN penetration. Under these circumstances, EPNs cannot exhibit high virulence on the targeted insect pest; therefore, they should be applied in combination with some of the other control agents. In this context, the main objective of this review was to summarize the current knowledge on the compatibility of EPNs with various agrochemicals and examine the interactions of EPNs and these agents in combined application against insect pests. This review highlighted firstly the growing research attention worldwide concerning the compatibility of EPNs with other control agents. Then, the compatibility of EPNs with synthetic insecticides of different classes was reviewed. In this regard, also, some special attention has been paid to herbicides, fungicides and nematicidal compounds as possible compatible agents to EPNs. Later on, the current review discussed the importance of EPN application in combination with different insect growth regulators, juvenoids, ecdysteroids and chitin synthesis inhibitors. An overview of agricultural management practices and soil amendments in relation to EPNs was provided including the compatibility of EPNs with organic and inorganic fertilizers. Some attention has been paid to the EPN tolerance and susceptibility to heavy metals and other soil chemical pollutants, and EPNs as good bio-indicators of the environmental pollutants. The last aspect was the compatibility of EPNs with crude plant extracts and isolated phytochemicals. In conclusion, a combination of EPNs with compatible agrochemicals is a promising approach to the pest control strategy. EPNs may be combined with various compatible agrochemicals with additive, or preferably synergistic, effects on pest mortality. For this purpose, also, the exposure period should also be taken into consideration, because the exposure of EPNs to agrochemicals for a prolonged exposure period may turn their interaction to antagonistic and subsequently low control efficiency against the targeted insect due to the reduction of the EPN viability and infectivity.

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INTRODUCTION

Indiscriminate and repeated use of synthetic insecticides usually leads to several serious problems, such as environmental hazards, detrimentally toxicological effects on humans and development of the insect resistance toward different insecticides of various classes (Rose, 2001; Davies *et al*., 2007; Mosallanejad and Smagghe, 2009; Yarahmadi *et al*., 2009; Sharifian *et al*., 2012). Besides contaminating the environment, including the soil and water, insecticide residues deleteriously affect the natural enemies and useful organisms like earth worms, bees, spiders, and plants (Costa *et al*., 2008; Aktar *et al*., 2009; Singh *et al*., 2014; Pertile *et al*., 2020; Pelosi *et al*., 2021). They also reduce some characteristics of animals, such as immunity to diseases, vitality, and the success of mating (Syromyatnikov *et al*., 2020). In addition, nutrient reduction and an increased disease incidence are quite common in crops grown on soils heavily treated with synthetic insecticides (Tripathi *et al*., 2020).

Therefore, biocontrol agents represent a better alternative to synthetic insecticides, because the bioagents are target-specific, easily biodegradable in the environment, and can be friendly used for sustainable pest management (Sayyed and Patel, 2011; Kumar and Singh, 2015; Kumar *et al*., 2021). The major groups of microorganisms, used as biocontrol agents, include some bacterial genera, fungal genera and entomopathogenic nematodes (EPNs), particularly those belonging to the families Steinernematidae and Heterorhabditidae (Chang *et al*., 2003; Sporleder and Lacey, 2021; Liu *et al*., 2021; Adeleke *et al*., 2022).

Entomopathogens that occur naturally are important control agents for controlling insect pests (Roy and Cottrell, 2008). The word "entomopathogens" was coined by Tanzini *et al*. (2001) to describe the microorganisms that regulate the populations of insect pests to the levels wherein no economic damage to economic plants is observed. Entomopathogens and their products are simple to produce and apply, highly effective, persistent, and eco-friendly (Ruiu, 2018; Ayilara *et al*., 2023) leading to acceptance of their worldwide use in pest management strategies (Lehr, 2014; Chattopadhyay *et al*., 2017; Chen, 2018; Essiedu *et al*., 2020; Essiedu *et al*., 2020; Liu *et al*., 2021). However, several authors (Chattopadhyay *et al*., 2017; Ruiu, 2018; Kumar *et al*., 2021; Ayilara *et al*., 2023) have preferred the term "Biopesticides" to describe several groups of biocontrol agents including the entomopathogens which are frequently reported to be an efficient tool for the insect pests.

For nematodes, the term "entomopathogenic" means (causing disease to insects) and is mainly used in reference to the endosymbiotic bacteria *Xenorhabdus* spp. (mutually associated with EPN *Steinernema* spp.) and *Photorhabdus* spp. (mutually associated with EPN *Heterorhabditis* spp.)(Boemare, 2002). These bacterial symbionts exist in the intestines of the infective juveniles (IJs) of EPNs. Once entering the body cavity of potential host larvae through the mouth, anus and spiracles or some membranous areas of the body wall, IJs release their symbiotic bacteria to attack the viscera of the insect, bring about general sepsis and then use putrefied organs of the insect as nutrients for EPNs (Adams and Nguyen, 2002). Also, these bacteria produce some toxins and share in the overcoming of the host's immune system and ultimately kill the insect host within 72 h (Simoes *et al*., 2000; Duchaud *et al*., 2003; Chaston *et al*., 2011). Thus, these symbiotic bacteria can be considered one of the main factors involved in EPN infectivity (Tarasco *et al*., 2023). For more detail, see reviews of Ghoneim and Bakr (2024) and Ghoneim and Hassan (2024).

Because of their traits and characteristics, such as adaptability to various habitats, wide range of insect hosts, excellent ability at searching hosts, easy mass production and ability to resist some chemical pesticides, EPNs can be considered excellent biocontrol agents over other agents against various insect pests, particularly of soil and cryptic habitats (Koppenhöfer *et al*., 2002; Shapiro-Illan *et al*., 2012; Kulkarni, 2017; Paunikarand Kulkarni, 2020; Yadav *et al*., 2023). One of the most important attributes of EPNs is their compatibility/tolerance to a number of biopesticides, insecticides herbicides, acaricides, nematicides, fertilizers and pathogens (De Nardo and Grewal, 2003; Koppenhofer and Grewal, 2005; Kulkarni *et al*., 2009; Paunikar *et al*., 2012; Laznik and Tredan, 2014; Chavan *et al*., 2018; Devi, 2019).

On the other hand, several environmental factors directly affect EPN populations in the soil, such as humidity and temperature (Dolinski *et al*., 2017), as well as environmental extremes or the resistance of certain insect pests to EPN penetration (Lewis *et al*., 2006; Georgis *et al*., 2006; Poinar and Grewal, 2012). Under these circumstances, the use of EPNs alone to control insect pests on foliage results in poor or moderate levels of pest control (Toepfer *et al*., 2014; Brida *et al*., 2018). The combination of EPNs with other control agents can enhance the control efficacy against the targeted pest, with greater cost-reduction in application time required (Koppenhofer and Grewal, 2005). In other words, EPNs can be applied in combination with other control agents as a strategy for providing cost-effective, time-saving and long-lasting pest control (Abd-Elgawad, 2019; Özdemir *et al*., 2020a). Thus, the main goal of this strategy is the enhancement of EPN effectiveness for more efficient control (Koppenhöfer and Grewal, 2005; Bajc *et al*., 2017). In this context, the main objective of the present review was to summarize the current knowledge on the compatibility of EPNs with various agrochemicals and examine the interactions of EPNs and various agrochemicals in combined application as a more efficient control strategy against insect pests.

1. Compatibility of EPNs with Other Control Agents- Growing Research Attention in the World:

Compatibility of EPNs with agrochemicals has been widely investigated in the world (Chen *et al*., 2003; Gutierrez *et al*., 2008; Laznik *et al*., 2012; Laznik and Trdan, 2014; Mahmoud *et al*., 2016; Garriga *et al*., 2019; Koppenhöfer *et al*., 2020; Kruk and Dziêgielewska, 2020; Askary and Ahmad, 2020; Nalinci *et al*., 2021 Kumar *et al*., 2022). It is important to point out that the EPN combinations with other control agents may result in additive, synergistic, or antagonistic interaction (De Nardo and Grewal, 2003; Laznik *et al*., 2012). A synergistic effect appears when two or more control agents combine to produce a greater effect than the effect if each agent was applied alone (Ansari *et al*., 2005, 2008; Devi, 2019). On the other hand, an antagonist interaction occurs when two control agents cancel or reduce each other out. Direct antagonism is the infection or predation of EPNs by another organism, whereas indirect antagonism occurs during competition (either interference or exploitation) for resources and spaces (Kaya, 2002). In addition, an additive effect of two or more control agents combines and produces a total effect equal to the sum of the effects of each individual agent in the reaction (Ansari *et al*., 2005, 2008; Mahmoud *et al*., 2016).

To understand this necessary approach for successful EPN application against insect pests, several environmental factors directly influence EPN populations in the soil, such as humidity and temperature (Dolinski *et al*., 2017), as well as environmental extremes or the resistance of certain insect pests to EPN penetration (Lewis *et al*., 2006; Georgis *et al*., 2006; Toepfer *et al*., 2014). As, other factors may affect the presence of the infective juveniles (IJs) of EPNs in the soil since these organisms live in an environment thatcontinuously receives the addition of agrochemical compounds that will influence their survival (Poinar and Grewal, 2012; Brida *et al*., 2018). Whereas, some authors (Sabino *et al*., 2017; Chergui *et al*., 2019) reported that IJs can remain viable when in contact with several chemical compounds.

Under these circumstances, the use of EPNs alone to control insect pests on foliage results in poor or moderate levels of pest control (Vyas *et al*., 2003). Combination of EPNs with other control agents can enhance the control efficacy against the targeted pest, with greater cost reduction in application time required (Koppenhofer and Grewal, 2005). In other words, EPNs can be applied in combination with other control agents as a strategy for providing cost-effective, time-saving and long-lasting pest control (Abd-Elgawad, 2019; Özdemir *et al*., 2020a). This promising approach is also called a ‘dual attack’ approach (Stiling, 1992). Therefore, many investigators have paid attention to evaluating the EPNs combinations with insecticides (Koppenhofer *et al*., 2000; Sheykhnejad *et al*., 2014), biocontrol agents (Koppenhofer *et al*., 1999; Wu *et al*., 2014), and parasitoids (Lacey *et al*., 2001; Atwa *et al*., 2013).

In this context, also, many studies have alsofound the IJs of EPNsaretolerant to short exposures (2-6 h) of many insecticides, acaricides, fungicides and herbicides and insect growth regulators (Laznik and Trdan, 2014). Therefore, EPN can be tank-mixed and applied together with such compounds (Koppenhöfer and Grewal, 2005; Radova, 2010; Viteri *et al*., 2018). This tolerance of IJsto insecticides may be due to the occurrence of two exterior epidermal layers, as well as the oral and anal apertures of IJs beingclosed during dormancy, preventing hazardous chemicals and other objects from entering their bodies (Campbell and Gaugler, 1991). These IJs do not eat during this period; therefore, their survival depends on internalenergy sources (reserves). IJs' ability to survive during the dormancy period is thus determined by their metabolism and internal energy reserves which support physiological and behavioral processes associated with environmental stress adjustment (Glazer, 2002).

2. Compatibility EPNs with Synthetic Insecticides:

2.1.Basic Knowledge:

Firstly, pesticides can be classified based on their active ingredients, functions, and sources. According to their active ingredients, pesticides are classified into organochlorines, carbamates, organophosphates, neonicotinoids, pyrethroids, *etc*. Functionally, they can be classified into insecticides, herbicides, fungicides, algicides, rodenticides, *etc*. According to their sources, pesticides are classified into synthetic pesticides and biopesticides (Ayilara *et al*., 2023).

Several studies have been conducted on whether insecticides can be combined with other ingredients, such as fertilizers, microbial control agents, and other chemical pesticides (Koppenhöfer *et al*., 2000; Gutiérrez *et al*., 2008; Laznik *et al*., 2012; Laznik and Trdan, 2014; Ulu *et al*., 2016; Şahin and Susurluk, 2018). Over the past few decades, there has been increasing evidence that the combinations of chemical insecticides with biocontrol agents represent a strategy to provide more effective pest control, particularly when both agents interact synergistically. One category of biocontrol agents that appear to be compatible with various chemical insecticides is EPNs (Koppenhofer and Grewal, 2005; Koppenhöfer and Fuzy, 2008; Khan *et al*., 2018). Therefore, several studies used the local EPN species and isolates to test their pathogenicity on serious insect pests and their compatibility with some registered pesticides to design more sustainable pest management programs (Baimey *et al*., 2015; Ferreira *et al*., 2016; Laznik and Trdan, 2017; Sabino *et al*., 2019; Khan *et al*., 2020; Özdemir *et al*., 2020b; Koppenhöfer *et al*., 2020).

Now, it is important to review the results of several studies focusing on this aspect of efficient control approach, since many EPNs belonging to the families Steinernematidae and Heterorhabditidae have been found to survive under exposure to different chemical pesticides (Koppenhöfer *et al*., 2002; De Nardo and Grewal, 2003; Schroer *et al*., 2005; Laznik *et al*., 2012; Laznik and Trdan, 2014; Ulu *et al*., 2016). For example, the compatibility of the EPNs *Steinernema* spp. and *Heterorhabditis* spp. with various insecticides has been extensively investigated by many researchers (Sunanda *et al*., 2014; Mohan, 2015; Kary *et al*., 2018; Hassan and Ibrahim, 2019; Sabino *et al*., 2019). Moreover, there are no difficulties in applying EPNs *via* different techniques and they can be combined with various chemical compounds (Mahmoud and Pomazkov, 2004; Mahmoud, 2007;

Lanzoni *et al*., 2014).

The available literature includes, also, a study on the direct application of the EPN *Steinernema carpocapsae* with pesticides at the recommended dose. The pesticides had no adverse effect on the EPN viability at room temperature after 3 h of exposure (Alumai and Grewal, 2004). Moreover, another study indicated that some chemical insecticides, at recommended doses, had no serious effect on EPN survival even after 72 h of exposure (Mahmoud *et al*., 2006). Similarly, De Nardo and Grewal (2003) investigated the compatibility of EPN *Steinernema feltiae* with different pesticides, in glasshouses. Based on their results, the EPN viability was more than 80% with all the pesticides even after 72 h of exposure.

For some detail, the combined application of a mixture of EPNs and some insecticides caused a significant increase in mortality of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae). A synergistic or additive effect can be expected between EPNs and the insecticides (Bernardi *et al*., 2010). Negrisoli *et al*. (2010) evaluated the efficacy of EPNs in combination with some insecticides to control the same insect pest in corn crops and recorded synergistic and additive interactions between EPN species and insecticides. According to Atwa (2013), the EPNs *Heterorhabditis bacteriophora* and *Steinernema* spp. were compatible with different pesticides tested against the Egyptian cotton leafworm *Spodoptera littoralis* (Lepidoptera: Noctuidae) and therefore EPNs-insecticide mixtures can be used in an integrated pest management (IPM) system.

Against the tomato leaf miner *Tuta absoluta* (Lepidoptera: Gelechiidae), EPN *S. carpocapsae* was effective outside the tomato leaves not inside. This may be due to the EPN susceptibility to some abiotic factors in addition to the presence of larvae within tunnels. In this case, EPN can be combined with a registered insecticide to facilitate or enhance its control effectiveness (Türköz and Kaşkavalci, 2016). Two years later, Sabino *et al*. (2018) evaluated the susceptibility of combined EPN *Heterorhabditis amazonensis* JPM4 with different insecticides to control the same insect in a tomato crop and recommended this approach for reducing the inappropriate use of insecticides against larvae. Also, El-Ashry and Ramadan (2021) reported that the efficacy of EPNs to control the scarab beetle *Pentodon bispinosus* (Coleoptera: Scarabaeidae) can be induced by the combination with commonly applied insecticides. For more examples, see Yan *et al*. (2012), Kulkarni *et al*. (2013), Patil *et al*. (2015), Gangadhara *et al*. (2019), Devi (2019), El-Ashry *et al*. (2020) and Khan *et al*. (2021).

Another point of concern in this context is the exposure period because some authors (Monteiro *et al*., 2014; Yadav *et al*., 2017; Khan *et al*., 2018) reported that the prolonged exposure period to the EPNs alone, and in combination with insecticides, have proven to increase mortality of the insect larvae (Monteiro *et al*., 2014; Yadav *et al*., 2017; Khan *et al*., 2018). However, this point of view will be discussed in the following section entitled *"Serious challenges of successful EPN-insecticide combinations"*.

It should be kept in mind that the main goal of this strategy is the enhancement of EPN effectiveness for more efficient control of certain insect pests on the plants (Negrisoli *et al*., 2010; Laznik *et al*., 2012; Laznik and Trdan, 2014; Monteiro *et al*., 2014; Yadav *et al*., 2017; Garriga *et al*., 2019; Koppenhöfer *et al*., 2020; Yan *et al*., 2020; Nalinci *et al*., 2021). In addition, this strategy has been applied to provide an understanding of how the naturally occurring EPN in soils can be better preserved in agroecosystems (Barbosa-Negrisoli *et al*., 2009; Yan *et al*., 2012; Yuksel *et al*., 2019).

2.2. EPN Compatibility with Insecticides of Class Organophosphates:

Globally, EPN compatibility has been tested with well over 100 different chemical pesticides (Vashisth *et al*., 2013). Through the following sections, we will review the currently available studies on EPN combinations with various registered insecticides according to the major classes. Based on the current literature, there is a growing attention of researchers worldwide for assessing the combinations of EPNs with different organophosphate insecticides. For instance, De Nardo and Grewal (2003) investigated the interaction between EPN *S. feltiae* and acephate. They recorded a compatibility with no loss in viability and infectivity up to 24 h of exposure and viability was more than 80% even after 72 h of exposure. Studies carried out by some investigators showed low IJ mortality of EPN *S. carpocapsae* when exposed to chlorpyrifos (Alumai and Grewal, 2004; Gutierrez *et al*., 2008). Similarly, many authors reported low IJ mortality of EPN *H. amazonensis* with certain insecticides including chlorpyrifos (Chen *et al*., 2003; Gutierrez *et al*., 2008; Kruk and Dziêgielewska, 2020). Also, Negrisoli *et al.* (2010) reported that chlorpyrifos was compatible with *H. indica, S. carpocapsae* and *S. glaseri* under laboratory conditions. In addition, chlorpyrifos-ethyldid not reduce the survival of EPNs *S. carpocapsae* and *S. glaseri* for the control of *S. frugiperda* (Monteiro *et al*., 2014; Ulu *et al*., 2016).

In a study of Negrisoli *et al*. (2010), the additive interaction between *S. carpocapsae* and chlorpyrifos, and the synergistic effect of chlorpyrifos with *S. glaseri*, were recorded for the control of *S. frugiperda*. They reported that the interactions of *H. indica, S. carpocapsae* and. *glaseri* with chlorpyrifos depended on the formulation and the tested concentration. In Egypt, Askary and Ahmad (2020) found the EPN *H. pakistanensis* (3.0 lakh IJs/m^2) + dichlorvos 76 EC (0.025%) causing the highest larval mortality (79.65%) of the cabbage butterfly *Pieris brassicae* (Lepidoptera: Pieridae) under field conditions. This result agreed with some reported results of several authors at lower doses and short-term exposure where EPNs were compatible with dichlorvos (Zhang *et al*.,1994). In a field study of Kumar *et al*. (2022), the EPN *Steinernema asiaticum*and malathion 50 EC, singly or in combination, were applied against the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) larvae. Depending on their results, the highest larval mortality (37.5%) was obtained by using EPN at 25,000 per plant in combination with half the recommended concentration of malathion (0.025%) leading to a synergistic effect. For more examples, see Table (1).

On the contrary, some reports indicated several organophosphate insecticides are very toxic to the survival of many EPNs of various families (Rovesti and Deseö, 1990; Gordon *et al*., 1996; Nishimatsu and Jackson, 1998; Shivamuthuprakash *et al*., 2011). For example, chlorpyrifos exhibited an undetectable effect on the viability of *S. feltiae* and *H. bacteriophora* (Peters and Poullot, 2004), but the susceptibility of *S. feltiae* was more affected than *H. bacteriophora* (Devindrappa *et al*., 2017; Raheel *et al*., 2017). Fenitrothion (Sumithion Super®) and chlorpyrifos (Dursban 10 G®) were tested by Nermuť and Mráček (2010) against certain steinernematid EPNs. These insecticides caused marginally lower infectivity of EPNs and higher EPN mortality, respectively, in comparison with different pesticides.

In Egypt, El-Ashry *et al*. (2020) evaluated the mixing of chlorpyrifos (Pestban 48% EC), chlorpyrifos (Tafaban 48% EC) and fenamiphos with five EPNs *S. carpocapsae*, *S. feltiae*, *S. glaseri*, *H. bacteriophora* and *H. bacteriophora* for the control of tomato fruit borer *Helicoverpaarmigera* (Lepidoptera: Noctuidae). Depending on their results, these pesticides with IJs of EPNs showed an additive or antagonistic interaction. Devi (2022) conducted a laboratory study to evaluate the compatibility of *H. bacteriophora* with "Tricel" (chlorpyriphos 20% EC), insecticidal compounds currently used against cutworm *Agrotis ipsilon* (Lepidoptera: Noctuidae). His results showed that the survival rate of EPN exposed to chlorpyriphos was reduced to 50%. Also, EPN infectious ability and reproduction rate in *A. Ipsilon* were reduced by exposure to chlorpyriphos. Combinations of *S. feltiae* or *S. carpocapsae* with sublethal concentrations of fenamiphos resulted in a reduction of the EPN infectivity. This may be due to the impaired ability of IJs to locate the host, affecting locomotion and possibly sensory perception, and therefore reducing EPN pathogenicity (Patel and Wright, 1996). For more examples, see Table (1).

Table 1. Compatibility of entomopathogenic nematodes (EPNs) with some organophosphate insecticides in combined applications.

EPN	Insecticide	Insect	Result	Reference(s)
Steinernema carpocapsae	Chlorpyrifos	*Spodoptera frugiperda*	Higher virulence	Negrisoli *et al.* (2010)
Heterorhabditis bacteriophora, H. indica and *Steinernema longicaudum*	Chlorpyrifos	*Holotrichia parallela*	Additive mortal effect	YuDong *et al.* (2012)
S. feltiae	Chlorpyrifos	*Spodoptera littoralis*	No adverse effect on survival but reduction of virulence	Gutiérrez *et al.* (2008)
Heterorhabditis amazonensis	Chlorphenvinphos and dichlorvos	*S.littoralis*	High mortality of larvae	Gutiérrez *et al.* (2008)
H. bacteriophora HB and Steinernema brazilense (IBCB-n06)	Malathion and Phosmet	*Ceratitis capitata*	The highest mortality of larvae	Jean-Baptiste *et al.* (2021)
Steinernema abbasi (CISH EPN-1)	Bifenthrin	*Galleria mellonella*	No adverse effect on EPN survival	Kesava *et al.* (2015)
H. amazonensis	Chlorphenvinphos and Dichlorvos	*S.littoralis*	High mortality of EPN	Chen *et al.* (2003), Gutierrez *et al.* (2008), Kruk and Dziêgielewska (2020)
H. bacteriophora (HP88 strain) and *S. carpocapsae* (All strains)	Fenamiphos		IJs mortality and reduced viability	El-Ashry and El-Marzoky (2018)
S. carpocapsae	Trichlorfon	*Spodoptera litura*	Reduced infectivity	Zhang *et al.* (1994)
H. bacteriophora HP88	Trichlorfon	*G. mellonella*	Reduced viability and pathogenicity	Alumai and Grewal, (2004)
S. abbasi (CISH EPN-1)	Dichlorvos	*G. mellonella*	Higher mortality of EPN	Kesava *et al.* (2015)

2.3. EPN Compatibility with Insecticides of Class Neonicotinoids:

Depending on the incubation period, as observed with *H. bacteriophora* agitated in solutions of imidacloprid for 24 h, no negative effect has been observed on the EPN survival and infectivity (Koppenhofer and Kaya, 1998). As evaluated by Alumai and Grewal (2004), imidacloprid exhibited no drastic effect on *H. bacteriophora* viability. Also, thiamethoxam and imidacloprid had no significant effects on *S. carpocapsae* pathogenicity. Moreover, imidacloprid, at the recommended rate (330/440 g AI/ha), significantly enhanced the *H. bacteriophora* pathogenicity at 500 and 300 L/ha application volumes. Although mixing imidacloprid (0.04:1.25%) with EPN *S. feltiae* SN caused 3.5% mortality (Patil *et al.*, 2015), the decreasing application rate of imidacloprid led to the enhancement of the EPN efficacy by deleting the toxic effect (Yan *et al.*, 2019). In their study, Wu *et al.* (2017) concluded that the combination of EPNs and thiamethoxam significantly increases the mortality (90%) of the subterranean insect*Bradysiaodoriphaga* (Diptera: Sciaridae) larvae for up to six weeks. To control the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae), Arshad *et al.* (2020) combined EPN *H. indica* with imidacloprid. Based on their results, the mortality rate in the early three larval instars and adults was the highest in combined treatments. Furthermore, egg hatching, pupation and adult emergence of this pest were considerably reduced in the combined applications. For more examples, see Table (2).

In contrast, Alumai and Grewal (2004) recorded a remarkable reduction of the *H. bacteriophora* viability in the last instar larvae of *G.mellonella* after treatment with thiamethoxam. Also, imidacloprid reduced the viability and infectivity of *S. carpocapsae* (Negrisoli Jr *et al*., 2008). El-Ashry and Ramadan (2021) studied the combined efficacy of EPNs, *H. Bacteriophora* (Ar-4) and *S. feltiae* (Filipjev) with imidacloprid against *P. bispinosus*. They observed no synergistic interaction in the combinations. However, the final interaction mainly depends on the chemical pesticide selectivity and toxicity to target insects (stage and instar). For more examples, see Table (2).

Table 2. Compatibility of EPNs with some neonicotinoid insecticides in combined applications.

EPN	Insecticide	Insect	Result	Reference(s)
H. bacteriophora and *S. feltiae*	Imidacloprid	*Planococcus ficus*	No negatively affected survival and infectivity of EPN	Le Vieux and Malan (2015)
H. sonorensis	Imidacloprid	*Helicoverpa zeae*	Antagonistic to the virulence	Navarro *et al.* (2014)
H. sonorensis	Dinotefuran	*H. zeae*	Additive interaction	Navarro *et al.* (2014)
S. carpocapsae and *H. bacteriophora*	Imidacloprid	*Agrotis ipsilon*	Induced EPNs efficacy	Mahmoud *et al.* (2016)
H. megidis, S. feltae and *S. glaseri*	Thiomethoxam	*Popillia japonica*	Compatibility	Koppenhofer *et al.* (2003)
S. carpocapsae	Thiomethoxam	*Galleria mellonella*	Compatibility	Alumai and Grewal (2004)
H. bacteriophora	Imidacloprid	*Holotrichi aoblita*	Synergistic or additive interaction	Viteri *et al.* (2018)
Heterrhabditis spp. and *S. glaseri*	Imidacloprid	*P. japonica*	Synergistic interaction	Koppenhofer *et al.* (2000)
H. bacteriophora and *H. zealandica*	Imidacloprid	*Agrotis orientalis* and *Cyclocephala borealis*	Compatibility	Koppenhofer and Fuzy, (2008)
H. amazonensis JPM4	Thiamethoxam	*Tuta absoluta*	Compatibility	Sabino *et al.* (2019)
H. bacteriophora HB and *S. brazilense* IBCB-n06	Thiamethoxam	*Ceratitis capitata*	Adversely affected viability and infectivity	Jean-Baptiste *et al.* (2021)
H. bacteriophora HB and *S. brazilense* IBCB-n06	Acetamiprid	*Ceratitis capitata*	Compatibility	Jean-Baptiste *et al.* (2021)
H. amazonensis	Imidacloprid or Thiamethoxam	*Dysmicoccus brevipes*	Reduced viability	Zart *et al.* (2021)

2.4. EPN Compatibility with Insecticides of Class Carbamates:

The carbamate insecticide oxamyl was found to synergistically improve the pathogenicity of *S. carpocapsae* against *A. segetum*, but only in a fumigated soil, probably by enhancing the EPN nictation behavior (Ishibashi, 1993). According to Alumai and Grewal (2004), carbaryl had no inhibitory effect on the viability of *H. bacteriophora*. Also, it did not adversely affect *S. carpocapsae* viability and pathogenicity when compared to the control, with over 96% EPN viability at all concentrations.

On the other hand, Rovesti *et al.* (1988) reported that the EPN combination with carbamate insecticides caused toxicity to *Steinernema* spp. and *Heterorhabditis* spp. The results of NermuťandMráček (2010) showed that EPNs *S. feltiae*, *S. arenarium* and *S. kraussei* were very resistant to some pesticides. The most toxic pesticides were Vydate® (oxamyl–carbamate) and Sulka® (sulphur). However, the Previcur® (propamocarb), for example, was not very toxic for steinernematids. This agreed with Gordon *et al*. (1996) who reported that not all carbamates are highly toxic to EPNs. Also, the latter researchers tested the toxicity of carbofuran against *S. carpocapsae* and *S. feltiae* and observed the death of IJs of both EPN species.

In addition, a reduction in the infectivity of *S. feltiae* and *S. carpocapsae* was recorded after exposure to sublethal concentrations of oxamyl. This may be due to the impairment of the IJs ability to locate the host, affecting locomotion and possibly sensory perception, and therefore reducing nematode pathogenicity (Patel and Wright, 1996). Also, the lowest infectivity of EPNs *S. feltiae*, *S. arenarium* and *S. kraussei* was observed in treatments with the oxamyl (Nermuť and Mráček, 2010). Some years later, the effect of oxamylon viability and infectivity of IJs of *H. bacteriophora* (HP88 strain) and *S. carpocapsae* (All strains) was assessed by El-Ashry and El-Marzoky (2018) against 6th instar larvae of *G. mellonella*. One day after treatment, the tested pesticide reduced the viability of IJs in different percentages depending on the EPN species. Moreover, IJs mortality was seriously increased with oxamyl, at the recommended doses, after two days.

2.5. EPN Compatibility with Insecticides of Class Pyrethroids:

Many authors (Koppenhöfer *et al*., 2002; Koppenhöfer and Fuzy, 2008; Sabino *et al*., 2014; El-Ashry and Ramadan, 2021) reported that several pyrethroids were considered non-toxic to EPNs. Although Head *et al*. (2000) reported that pyrethroids have strong influences on the infectivity of some EPNs but not viability, NermuťandMráček (2010) described the very low influence of pyrethroids on both mortality and infectivity of *S. feltiae*, *S. arenarium* and *S. kraussei*. Specifically, deltamethrin did not reduce the survival of EPN species (Monteiro *et al*., 2014; Can Ulu *et al*., 2016). Moreover, the *S. carpocapsae* combination with cypermethrin had high efficiency against *S. frugiperda* (Negrisoli *et al*., 2010). Similarly, some commercial formulations of cypermethrin were reported to be harmless to the survival or infectivity of EPNs (Yan *et al*., 2012). Also, some pyrethroids, such as deltamethrin, lambda-cyhalothrin, cypermethrin, and permethrin, were found compatible with *H. indica*, *S.carpocapsae* and *S. glaseri*, under laboratory conditions (Negrisoli *et al*., 2010).

Some years later, Kesava *et al*. (2015) evaluated the compatibility of indigenous EPN *S. abbasi* (CISH EPN-1) with lambda-cyhalothrin 5% EC and bifenthrin 8% SC), at field-recommended doses, against *G. mellonella* under laboratory conditions. Based on their results, IJs retained their ability to infect the last instar larvae of *G. mellonella* after exposure to bifenthrin and lambda-cyhalothrin, thus, exhibiting good compatibility and favoring*S. abbasi* as a potential EPN against mango pests. In a study of Sinhouenon *et al*. (2019) on *P. xylostella* in northern Benin, lambda-cyhalothrin displayed negligible effects on the survival of EPNs *Steinernema* sp. 83a and *H. sonorensis* KF723827. For controlling the cigarette beetle *Lasioderma serricorna* (Coleoptera: Anobiidae), El-Ashry and Hegab (2021) investigated the compatibility of the native *H. bacteriophora* (Ar-4 strain) and imported *H. bacteriophora* (HP88 strain) with different applications of lambda-cyhalothrin. They concluded that the best interaction was obtained with the quarter-recommended application (0.25 RC) of lambda-cyhalothrin when combined with EPNs at 100 IJs/larva, which displayed a synergistic effect. Under laboratory conditions, El Roby *et al*. (2023) evaluated the activity of two EPNs, *H. bacteriophora* (HP88) and *S. carpocapsae* (AT4), as well as their compatibility with lambada cyhalothrin and flubendiamide against 4th instar larvae of *S. frugiperda*. Their results indicated that the combination of all insecticides with two EPN strains was synergistic against 4th instar larvae.

In contrast, *S. carpocapsae* was reported to be more susceptible to deltamethrin compared to *H. bacteriophora* and *H. indica* (Negrisoli *et al*., 2010). Also, the joint action of EPNs*S.carpocapsae* (All strain), *S. feltiae* (Filipjev), *H. bacteriophora* (HP88), and *H. bacteriophora* (Ar-4) and lambda-cyhalothrin were evaluated by Aioub *et al*. (2021) against 4th instar larvae of the cabbage white butterfly *Pieris rapae* (Lepidoptera: Pieridae) under laboratory conditions. Their results demonstrated the interaction of *S. feltiae* (Filipjev) with the tested insecticide at LC.sub.$_{50}$ exhibited an antagonistic effect on the mortality of 4th instar *P. rapae* larvae after 3 days of treatment.

2.6. EPN Compatibility with The Oxadiazine Pesticides:

Recent studies have shown that EPNs were compatible with many oxadiazine pesticides and their combinations resulted in more efficient control of several insect pests. For example, the EPN *S. carpocapsae* was not effective against *T. absoluta* larvae but treatment of *S. carpocapsae* in combination with insecticide indoxacarb, *S. carpocapsae* could adversely affect the targeted insect (Al-kazafy *et al*., 2016). According to Khan *et al*. (2021), indoxacarb caused high mortalities (90–92%) of the tobacco cutworm *Spodoptera litura* (Lepidoptera: Noctuidae) larvae after 72 h when applied in combination with *H. indica*. Depending on their results, also, a combination of indoxacarb with *S. carpocapsae* caused 90% mortality of *S. litura* larvae. On the other hand, indoxacarb caused less than 10% mortalities in both EPNs after 72 h of exposure. Based on the results of Aioub *et al*. (2021), the interaction between indoxacarb (at LC.sub.$_{50}$) and EPNs*S.carpocapsae* (All strain), *S. feltiae* (Filipjev), *H. bacteriophora* (HP88), and *H. bacteriophora* (Ar-4), showed additive effects on 4th instar *P. rapae* larvae. Indoxacarb (at LC.sub.$_{25}$) with *H. bacteriophora* (Ar-4) showed a potentiating effect. On the other hand, the interaction of *S. feltiae* with the tested insecticide at LC.sub.$_{50}$ exhibited an antagonistic effect on the mortality of the insect larvae after 3 days of treatment.

2.7. EPN Compatibility with Insecticides of Class Ryanoids/Diamides:

As shown in the available literature, some commercial formulations of chlorantraniliprole were reported to cause no harm to the survival or/and infectivity of EPNs (Yan *et al*., 2012). For example, combinations of *H. bacteriophora* with chlorantraniliprole demonstrated synergistic or additive interactions against 2nd instar larvae of the white grub *Holotrichia oblita* (Coleoptera: Scarabaeidae) and caused faster larval mortality than the EPN or insecticide alone (Guo *et al*., 2016). The combined application of *S. carpocapsae* and *H. bacteriophora* with chlorantaniliprole (Coragen) (at LC_{25}**)** led to high mortality of *S. littoralis* (Hassan and Ibrahim, 2019). In Egypt, El-Ashry *et al*. (2020) evaluated the possibility of mixing flubendiamide (Takumi 20% WG)} with five EPNs for the control of *H. armigera*. Depending on their results, an additive effect was observed in flubendiamide combinations with *S. glaseri, S. carpocapsae,*or *H. bacteriophora* (HP 88). In Turkey, Özdemir *et al*. (2021) evaluated the combined usage of *S.feltiae* KV6 Turkish isolate with chlorantraniliprole to control the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) larvae. According to their results, the tested insecticide showed no adverse effect on the survival and infectivity of the EPN isolate. In the year, Fubendiamide caused high mortalities (90–92%) of *S. litura* larvae after 72 h when applied in combination with *H. indica* (Khan *et al*., 2021).

On the contrary, some studies revealed the incompatibility of some EPNs with a number of insecticides belonging to this class. For example, a combination of *S. carpocapsae* with chlorantraniliprole has been suggested as the least toxic control strategy against *S. frugiperda* (Viteri *et al*., 2018). In a study to control the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae) by EPNs, cyantraniliprole formulation seriously affected the viability of IJs of *S. feltiae* and *Heterorhabditis* spp. (IBCB-n 46), mainly after 48 h of exposure (Guide *et al*., 2018). Also, El-Ashry *et al*. (2020) recorded an antagonism interaction between all flubendiamide combinations and *S. feltiae* or *H. bacteriophora* (Ba-1) against the *H. armigera* larvae.

2.8. EPN Compatibility with Insecticides of Other Classes:

With regard to phenylpyrazoles, Al-kazafy*et al*. (2016) found *S. carpocapsae* not effective alone against *T. absoluta* larvae but it was virulent in combination with the chemical insecticide fipronil. Fipronil had been reported as compatible with *H. Bacteriophora* Poinar and *S. carpocapsae* Weiser since they are highly resistant to fipronil but *S. arenarium* (Artyukhovsky) showed a mortality rate of 94.6 % after 24 h exposure (del Pino and Jové, 2006). Some commercial formulations of fipronil were reported to cause no harm to the survival and infectivity of different EPNs (Yan *et al*., 2012).

The available literature contains, also, diverse results of studies focusing on the compatibility of EPNs with insecticides of classes other than those mentioned in the previous sections. For instance, Cartap hydrochloride (an insecticide of the Nereistoxin analogue group) had been found to be highly toxic to EPNs *S. carpocapsae* (Zhang *et al*., 1994), *H. indica* and *Metarhabditisamsactae* (Prasad *et al*., 2016). Also, Chavan *et al*. (2018) evaluated the compatibility of EPN *H. indica* with different insecticides under laboratory conditions. Their results showed that *H. indica*is compatible with all insecticides except cartap hydrochloride. Sabino *et al*. (2019) investigated the compatibility of EPN *H. amazonensis* JPM4 with the registered insecticide Premio$^{®}$ for the control of *T. absoluta*in the tomato crop. Depending on their results, EPN was compatible with the tested insecticide and increased larval mortality. Later on, Özdemir *et al*. (2021) evaluated the combined usage of PBO (Piperonyl butoxide), DEM (Diethyl maleate) and DEF (S, S, S-tributylphorotrithioate) with *S. feltiae*for control *L. decemlineata*. These insecticides showed no adverse effect on the survival and infectivity of *S. feltiae* and the EPN isolate was considered compatible with integrated *L. decemlineata* control. This study also showed that pre-treatment with synergistic chemicals (particularly PBO and DEM) increased the efficacy of *S. feltiae* against *L. decemlineata*.

2.9. EPN Compatibility with Some Herbicides:

The majority of studies investigating the influence of herbicides on EPNs indicated that they have no drastic effects on different EPNs (Gibb and Buhler, 1998; Fujiie *et al*., 1993). For instance, the herbicide glyphosate was reported to be compatible with *H. bacteriophora* (Rovesti *et al*., 1988), *S. carpocapsae* and *S. feltae* (Rovesti and Deseö, 1990). De Nardo and Grewal (2003) assessed the compatibility of *S. feltiae* Filipjev with the herbicide clethodim (Envoy). They determined compatibility with no loss in viability and infectivity of EPN up to 24 h of exposure. Also, they found the viability of *S. feltiae* was more than 80% even after 72 h of exposure. Some years later, Laznic and Trdan (2017) reported no detrimental effect of the herbicide 2,4-D Sodium on the viability of *S. feltae*. Also, Chavan *et al*. (2018) evaluated the compatibility of EPN *H. indica* with some herbicides under laboratory conditions. Their results showed that *H. indica* is compatible with the majority of these herbicides. Sabino *et al*. (2019) investigated the compatibility of EPN*H.amazonensis* JPM4 with the registered herbicide Warrant$^{®}$ for the control of *T. absoluta* in the tomato crop. Depending on their results, EPN was compatible with the tested herbicide and increased larval mortality.

On the other hand, Gupta and Siddiqi (1999) reported that the herbicide 2,4-D Sodium was not compatible with *S. carpocapsae*. Trifluralin (Treflan 48 EC$^{®}$) has caused high mortality of EPNs *S. feltiae, S. arenarium* and *S. kraussei*, although this may be the result of the strong organic solvent and methanol contained in this herbicide (Nermuť and Mráček, 2010). Under laboratory conditions, Chavan *et al*. (2018) found incompatibility of EPN *H. indica* with pendimethalin. Then, Zart *et al*. (2021) evaluated the performance of nine isolates of *H. amazonensis* and one of *H. indica* on the mealy bug *Dysmicoccus brevipes*

(Hemiptera: Pseudococcidae). In the compatibility test, isolate NEPET11 (*H. amazonensis*) exhibited reduced viability due to the herbicide Poquer (Clethodim).

2.10. EPN Compatibility with Some Fungicides:

Many investigators have assessed the compatibility of some EPN species with a number of fungicides. In a study of the compatibility of *H. bacteriophora* HP88 and *S. carpocapsae* All strains with selected insecticidal compounds against the last instar larvae of *G. mellonella*, the fungicide mefenoxam had no significant effect on the viability of EPNs, with over 96% EPN viability in all concentrations (Alumai and Grewal, 2004). Also, Radova (2010) determined the survival and infectivity of IJs of *S. feltiae* after being exposed to some fungicides, *viz*., Candit (kresoxim-methyl), Captan, Teldor (Fenhexamid), and Tridal (Nuarimol), under laboratory conditions. They found the EPN tolerant to all tested fungicides, mortality during 72 h varied from 7.04% to 8.86%. The EPN reproduction was not influenced by the tested fungicides. Also, these fungicides had slight effects on *S. feltiae* virulence after 3 days. These results suggested that *S. feltiae* can be applied in combination with all tested fungicides.

On the contrary, De Nardo and Grewal (2003) recorded significantly reduced viability of *S. feltiae*by exposure to Terrazole® (10%) within 24 h compared to the controls. Also, the pathogenicity of *S. carpocapsae* and *H. bacteriophora* was significantly reduced by aluminum tris (a fungicide, Fosetyl-Al)(Alumai and Grewal, 2004). The fungicide mankozeb (Novozir MN 80®) caused higher mortality and lower infectivity of EPNs *S. feltiae*, *S. arenarium* and *S. kraussei* (Nermuť and Mráček, 2010). The compatibility of *H. indica* with different fungicides was evaluated under laboratory conditions by Chavan *et al*. (2018). Their results showed that the EPN was compatible with all compounds except the fungicides tricyclazole and carbendazium+mancozeb.

2.11. EPN Tolerance To Some Nematicidal Compounds:

It is well known that the nematicidal compounds have been used to control the plant-parasitic nematodes. In addition, some investigators have studied their effects on some EPNs. For instance, El-Ashry *et al*. (2020) studied the possibility of mixing fenamiphos (Dento40% EC) with five EPNs. They reported that the tested compound with IJs of EPNs showed an additive or antagonistic reaction with no evidence of synergistic action. One year later, Touray *et al*. (2021) investigated the effects of four registered nematicidal compounds (fluopyram, fosthiazate, metam potassium and fenamiphos) on the survival, virulence, penetration efficiency and reproduction of *S. carpocapsae* and *H. bacteriophora*. EPN survival suffered ≥ 80% mortality by fosthiazate, fenamiphos and metam potassium within 24 h.

2.12 Some Insights Into Effective EPN-Insecticide Combinations For Highly Efficient Pest Control:

Scavenging BehaviorAnd Fitness of EPNs in Relation To Insecticides:

As reported by Blanco-Pérez *et al*. (2019), EPNs can play a dual role in the environment as pathogens and as scavengers; both roles may contribute to the EPN population level in the environment. It has been evidently demonstrated that EPNs of the family Steinernematidae preferentially scavenged on recently dead insects (cadavers) that were yet to be colonized by other competitors (San-Blas and Gowen, 2008). In such hosts, these EPNs do not need to overcome the insect immune system or defense strategies. On the other hand, EPNs of the family Heterorhabditidae were less disposed to such behavior than steinernematids. This scavenging behavior could serve as a method to maintain the natural EPN populations as often times insects are partially eaten by natural enemies, or killed by pesticides (San-Blas and Gowen, 2008; Blanco-Pérez *et al*., 2019). Moreover, EPNs can penetrate and develop in both dead and live insects exposed to chemical insecticides. On the other hand, it is not exactly known that the chemicals that persist in the tissues of insects killed by insecticides may be toxic to the developing IJs of EPNs and their symbiotic bacteria (Puza and Mracek, 2010). Afterward, Nalinci *et al*. (2021) hypothesized that chemical insecticides have negative impacts on scavenging EPNs. In their study, they concluded that the fitness of scavenging IJs is not reduced by insecticides in insect cadavers. Furthermore, exposure to insecticides may promote the virulence of EPNs in some cases (Nalinci *et al*., 2021).

Serious Challenges of Successful EPN-Insecticide Combinations:

In this context, also, some challenges should also be taken into account since many insecticides did not interact with some EPN species while other insecticides enhanced the EPN efficacy (synergistic interaction)(Koppenhöfer and Kaya, 1998; Mannion *et al*., 2000; Kary *et al*., 2018). Also, some studies indicated the detrimental impacts of some insecticides on the EPN efficiency, in terms of infectivity and survival, against several insect pests (antagonistic interaction**)** (Gordon *et al*., 1996; Krishnayya and Grewal, 2002). For instance, different interactions have been reported for chemical insecticides with *S. carpocapsae* and *H. indica* after 48 h of exposure. By increasing exposure time to 96 h, the interactions of EPNs and insecticides turned antagonistic and can reduce the EPN viability and infectivity (Head *et al*., 2000; Krishnayya and Grewal, 2002; Negrisoli *et al*., 2010). Moreover, other studies have shown that delayed exposure to certain insecticides at higher concentrations can cause variable toxicity against EPNs *S. carpocapsae* and *H. indica* (Khan *et al*., 2018). The long combination periods between EPNs and chemical insecticides will show different types of toxicological interactions (Koppenhofer *et al*., 2000). Therefore, some authors (Kwizera and Susurluk, 2017; Mohankumar *et al*., 2017) have paid attention to the combination period of EPNs with insecticides, sincesome insecticides exhibited high compatibility with EPNs less than 96 h of treatment but long combining time will show toxic effect leading to increasing mortality of both EPN and insect host.

A great effort has been exerted in the world to handle the aforementioned challenges, since the extent to which EPNs interaction with chemical pesticides depends on a number of factors, including EPN species, rates and timing of application, developmental stage of the targeted pest, exposure method and the environmental complexity in which the interaction takes place (Kary *et al*., 2021). Furthermore, the life stage and instar of the targeted insect interfere with the compatibility of EPN with insecticides because the early larval instars of white grubs, for instance, are more susceptible to EPNs (Koppenhofer and Fuzy, 2008; Malinowski, 2011; Patil *et al*., 2017; Kary *et al*., 2018). Furthermore, the EPNs survival and efficacy were also affected by host traits, e.g. host species, host developmental stage, host's immune system, and molecules emitted by the host, so, changing EPN pathogenicity in the presence of chemical insecticides may be due to poor viability or mortality of IJs (Labaude and Griffin, 2018).

In addition, the EPN species differ in their susceptibility and sensitivity to different formulations of the same chemicalpesticide (Grewal, 2002). The actual concentration of the chemical to which the EPNs will be exposed will vary depending on the application volume and system used (Alumai and Grewal, 2004). The incompatibility of EPNs with certain insecticides may be attributed to the toxicity of the pesticide ingredient, consequently reducing their ability to infect the target host. It is also possible that the pesticide formulations could have detrimental toxic effects on the endosymbiotic bacteria associated with these EPNs as well, subsequently decreasing EPN infectivity (Alumai and Grewal, 2004).

As previously mentioned, some chemicals**,** used as inert ingredients or adjuvants in formulations, can be toxic to EPNs, hence compatibility of each formulation with the specific EPN species should be evaluated thoroughly (Krishnayya and Grewal, 2002; Radova, 2010). In other words, the compatibility of different chemicals and EPN strains/isolates should be extensively assessed to achieve good pest control (Devi, 2022). Another point of concern is the compatibility of EPNs with several insecticide scans achieved usually at lower doses and short-term exposures, they can be tank-mixed for application together in the field against targeted insect pests (Priya and Subramanian, 2008; Laznik and Trdan, 2014). Prior to use, compatibility and potential for tank-mixing should be based on manufacturer recommendations (Vashisth *et al*., 2013).

In summary, compatibility of EPNs with synthetic insecticides may help to preserve and maintain EPNs in the environment and favor biological pest control, *i.e*., EPNs may be utilized in synergy, when combined with insecticides that increase their control efficiency (Negrisoli Jr. *et al*., 2008, Leite *et al*., 2012, Tavares *et al*., 2012, Bajc *et al*., 2017). Also, EPN combined with certain doses of registered insecticide are easy to apply in the field, as they are easily sprayed using standard equipment including pressurized, mist, fan, electrostatic and aerial sprayers (Radova, 2010; Viteri *et al*., 2018).

In the same regard, some special attention should be paid to the sensitivity of certain insecticides or certain formulations of an insecticide to avoid a decrease in the EPN vitality and infectivity (Grewal *et al*., 1998; Head *et al*., 2000; Krishnayya and Grewal, 2002). Furthermore, some EPN species have varied susceptibility to different chemical pesticide formulations. This could be related to changes in the epidermal structure of IJs of different EPN species (Grewal, 2002). Moreover, some chemicals, used as inert ingredients or adjuvants in formulations, can be toxic to EPNs, hence compatibility of each formulation with the specific EPN species should be extensively evaluated (Krishnayya and Grewal, 2002). Because the EPN-pesticide compatibility can be strain-specific (Laznik *et al*., 2012), the species, strain, or isolate of EPN appear to be of great importance in determining its level of susceptibility to systemic insecticides (Koppenhöfer and Grewal, 2005; Laznik *et al*., 2012; Atwa *et al*., 2013). It is still necessary to test the compatibility of the commonly used pesticides in the area where EPN strains are anticipated to be used (Baimey *et al*., 2015; Sinhouenon *et al*., 2019).

3. Interaction of EPNs with Insect Growth Regulators - Competitive Or Complementary?

3.1. Insect Growth Regulators – A Synopsis:

Insect growth regulators (IGRs), or insect growth disruptors, have been used for insect pest control as an effective alternative to synthetic insecticides which usually lead to several drastic problems, such as environmental hazards, destruction of natural enemies, serious toxicological problems to humans and development of the insect resistance toward different insecticides (Rose, 2001; Davies *et al*., 2007; Costa *et al*., 2008; Mosallanejad and Smagghe, 2009; Yarahmadi *et al*., 2009; Sharifian *et al*., 2012). This term implies that IGRs are selective and specific to the target pests (Ishaaya *et al*., 2005; Horowitz *et al*., 2009; Sarwar, 2015), do not accumulate in the environment, are less toxic to man and domestic animals, less toxic to natural enemies and non-target organisms, and less persistent in the ecosystems (Mondal and Parween, 2000; Raslan, 2002; Taleh *et al*., 2015).

Therefore, IGRs can be used in the development of sustainable agriculture (Zhou *et al*., 2003; Wang and Wang, 2007; Sabry and Abdu, 2016). Also, there are many reports on the use of IGRs against insect vectors of human and animal diseases (Ijumba*et al*., 2010; Belinato *et al*., 2013). Based on the specific mode of action, IGRs have been categorized into three categories: (i) juvenile hormone analogues, JHAs, also called Juvenoids), (ii) Ecdysteroid agonists and (iii) Chitin synthesis inhibitors (CSIs) or moult inhibitors (Oberlander and Silhacek, 2000). They had been, also, grouped into CSIs and substances that interfere with the action of insect hormones (*i.e*. JHAs, and ecdysteroids)(Tunaz and Uygun, 2004).

***Juvenoids or JHAs*:**

They can be further classified into two groups: the terpenoid JHAs such as methoprene, hydroprene and kinoprene and the phenoxy JHAs such as fenoxycarb and pyriproxyfen (Dhadialla *et al*., 2005). Interestingly, several thousand synthetic compounds with JH-like effects have been described (Henrick, 2007; Ramaseshadri *et al*., 2012), many of which are structurally distinct from the native hormone (Jindra and Bittova, 2020). Starting from the mid-1970s, some of these "Juvenoids" have found commercial use, among the new class of insecticides, IGRs, or insect growth disruptors (Minakuchi and Riddiford, 2006; Pener and Dhadialla, 2012). Since JH does not occur in vertebrates, the juvenoid IGRs are considered safe for humans (Jindra and Bittova, 2020). According to the current literature, many Juvenoids have been reported as potential control agents against different insect pests *via* disruption of their survival, growth, development, reproduction and embryogenesis (Oberlander *et al*., 1997; Segura *et al*., 2009; Abdelhamid *et al*., 2019).

Ecdysteroids or Ecdysone Agonists:

Like other IGRs, ecdysone agonists act more slowly than neurotoxic insecticides because they disrupt the hormonal system or the physiological development of insects rather than directly killing these insects (Biddinger *et al*., 2006). Several substituted dibenzoylhydrazines that act as non-steroidal ecdysteroid agonists have been synthesized, such as the prototype compound RH-5849 (1,2-dibenzoyl-1-tert-butylhydrazine), Tebufenoside (RH-5992), Methoxyfenozide (RH-2485) and Halofenozide (RH-0345) and Chromafenozide (ANS-118), and used for controlling lepidopterous and coleopterous pests (Ishaaya, 2001; Palli and Retnakaran, 2001; Yanagi *et al*., 2006). These compounds are harmless to vertebrates (Carlson *et al*., 2001) with little or no adverse effects on beneficial insects (Retnakaran *et al*., 2003). Ecdysone agonists have a narrow spectrum of activity, a positive ecotoxicological profile, and short persistence in the environment (Sundaram *et al*.,2002, Osorio *et al*., 2008). These advantages make these compounds promising against many economically important agriculture and forest pests (Smagghe *et al*., 2003, Biddinger *et al*., 2006; Dhadialla and Ross, 2007; Pineda *et al*., 2009).

Chitin Synthesis Inhibitors:

Chitin synthesis inhibitors (CSIs), such as the Benzoylphenyl Urea compounds (BPUs), are compounds that inhibit the chitin biosynthesis in the larval stage of the insect, leading to abnormal endocuticular deposition and abortive molting, thus preventing molting, or produce an imperfect cuticle resulting in death (Mondal and Parween, 2000; Dhadialla *et al*., 2005; Yu, 2008; Merzendorfer, 2013). CSIs have received great attention in insect pest control strategies because of their unique action in interfering with chitin synthesis (Belinato *et al*., 2013). They are less toxic compounds to the non-target organisms and beneficial biota (Cutler and Scott-Dupree, 2007), exhibit very low mammalian toxicity (Barazani, 2001; Ishaaya and Horowitz, 2002), and have no residual effects (Talikoti *et al*., 2012).

After the discovery of Diflubenzuron (Dimilin), an array of new analogues (dimiloids) was synthesized by different agrochemical companies. These compounds include Chlorfluazuron (Atabron), Flufenoxuron (Cascade), Hexaflumuron (Consult), Lufenuron (Match), Teflubenzuron (Nomolt) and Triflumuron (Alsystin), *etc*. (Tomlin, 2000; Kim *et al*., 2000). In the few past decades, some new BPU analogues were developed, such as: Novaluron, Bistrifluron, Flucycloxuron, Hexaflumuron, Fluazuron, Buprofezin, CyromazineandNoviflumuron (Sheets *et al*., 2000; Karr *et al*., 2004; Sun *et al*. 2015). According to the aforementioned categorization of these compounds, the available studies concerning the combination of EPNs with IGRs can be reviewed below.

3.2. Compatibility of EPNs with JHAs:

Limited knowledge exists in the current literature on the assessment of compatibility of EPNs with JHAs. The compatibility of the EPN *S. feltiae* Filipjev with fenoxycarb (Precision 25WP) was studied by De Nardo and Grewal (2003). They recorded a compatibility with no loss in viability and infectivity of the EPN up to 24 h of exposure. Moreover, viability was more than 80% even after 72 h of exposure. Some years later, Radova (2010) determined the survival and infectivity of *S. feltiae* IJs after exposure to Admiral (pyriproxyfen) and Enstar (kinoprene), under laboratory conditions. Their results indicated that *S. feltiae* was tolerant to the tested IGRs, and low mortality during 72 hs varied from 2.26% to 18.68%. Also, EPN reproduction was not influenced by these IGRs. These results suggested that *S. feltiae* can be applied in combination with the tested JHAs.

On the contrary, certain EPN species were incompatible with some JHAs, as reported by a number of studies. Gordon *et al*. (1996) tested the toxicity of fenoxycarb against the EPNs *S. carpocapsae* and *S. feltiae* and reported that this JHA caused the death of IJs of both EPN species. More than two decades later, Zart *et al*. (2021) evaluated the performance of nine isolates of *H. amazonensis* and one of *H. indica* on the mealybug *Dysmicoccusbrevipes* (Hemiptera: Pseudococcidae). In their compatibility test, the isolate NEPET11 (*H. amazonensis*) exhibited reduced viability due to the combination with Tiguer 100 EC (pyriproxyfen).

3.3. Compatibility of EPNs with Ecdysteroid Compounds:

Depending on the currently available literature, very few studies have examined the compatibility of EPNs with ecdysteroids or ecdysone agonists. Mannion *et al*. (2000) conducted laboratory bioassays to investigate the potential interaction between EPN *H. marelatus* IN strain and the ecdysteroid halofenozide against 3rd instar larvae of Japanese beetle *Popillia japonica* (Coleoptera: Scarabaeidae). According to their results, no synergism was detected in the combined treatments but no significant differences in EPN reproduction in larvae exposed to halofenozide and EPNs versus larvae exposed to only EPN. Later on, Alumai and Grewal (2004) evaluated the compatibility of *H. bacteriophora* HP88 and *S. carpocapsae* All strains with halofenozide in tank-mixes under laboratory conditions after culturing IJs in the last instar larvae of the greater wax moth *Galleria mellonella* (Lepidoptera: Pyralidae). This IGR significantly reduced the pathogenicity of *H. bacteriophora* only but had no significant effect on its viability. This IGR did not have a remarkable effect on *S. carpocapsae* viability.

Some years later, Radova (2010) determined the survival and infectivity of *S. feltiae* IJs after being exposed to some IGRs, *viz*., Mimic (tebufenozide) and Runner (methoxyfenozide), under laboratory conditions. This EPN was tolerant to these ecdysteroids, and mortality during 72 h varied from 2.26% to 18.68 %. According to the results of the same study, EPN reproduction was not affected by these IGRs. In conclusion, results revealed a tolerance of *S. feltiae* to the tested compounds. The Methoxyfenozide was found harmless to two *H. indica* and *S. carpocapsae* even 96 h after treatment of *S. litura* larvae while the lowest larval mortality (44.00±3.74%) of the targeted insect was observed for a mixture of *H. indica* with Methoxyfenozide (Khan *et al*., 2021).

3.4. Compatibility of EPNs with CSIs:

In comparison with the previously mentioned IGR categories, the current literature contains results of many studies regarding the compatibility bioassays of EPNs with CSIs. For example, diflubenzuron was reported with no adverse effect on the survival and reproduction of *S. carpocapsae* (Hara and Kaya, 1982) and the viability of EPN *H. bacteriophora* (Rovesti *et al*., 1988). De Nardo and Grewal (2003) assessed the compatibility of *S. feltiae* Filipjev with diflubenzuron (Adept® IGR) and recorded compatibility of EPN with no loss in its viability and infectivity up to 24 h of exposure. Several years later, Sabino *et al*. (2014) studied the compatibility of *S. carpocapsae* All and *H. amazonensis* JPM4 with different compounds, including Certero® (triflumuron), against *G. mellonella* larvae. Depending on their results, triflumuron was found among the least toxic compounds on these

EPNs. The two EPN species were presented in sensitivity to this CSI. This result was in agreement with the results reported by Rovesti and Deseo **(**1990) on *S. carpocapsae* and *S. feltiae*.

Under laboratory conditions, Radova (2010) determined the survival and infectivity of IJs of *S. feltiae* after exposure to Match (lufenuron). They found *S. feltiae* tolerant to this CSI and its reproduction was not influenced. These results suggested that *S. feltiae* can be safely applied in combination with lufenuron. In another study, Negrisoli *et al*. (2010) found *H. indica, S. carpocapsae* and *S. glaseri* compatible with the CSIs lufenuron, diflubenzuron and triflumuron against *S. frugiperda* under laboratory conditions. Results of the same study revealed that *S. carpocapsae* in combination with Match™ lufenuron (0.150 L/ha) caused 90.0% larval mortality. Also, the interaction of lufenuron with *S. glaseri* was synergistic but dependedon the formulation and the tested concentration. According to the results of Negrisoli *et al*. (2010), EPNs, *H. indica, S. carpocapsae* and *S. glaseri* were compatible with CSIs Dimilin™ (diflubenzuron) and Certero™ (triflumuron), under laboratory conditions.

A decade later, Paunikar and Kulkarni (2020) evaluated the compatibility of IJs of *S. dharanaii* (TFRIEPN-15) with Cigna® (lufenuron) and recorded no detrimental effect on the survival, infectivity and progeny production of the EPN. Another CSI, Novaluron, was found harmless against *H. indica* and *S.carpocapsae* even 96 h after treatment of *S. litura* larvae (Khan *et al*., 2021). As recorded by Jean-Baptiste *et al*. (2021), *H. bacteriophora* HB and *S. brazilense* (IBCB- n06) were compatible with Novaluron for the control of the fruit fly *Ceratitis capitata* (Diptera: Tephritidae), with the highest mortality of the targeted fly occurring in a combination of either EPN with the tested compound, followed by EPN or CSI alone.

In Egypt, Hassan and Ibrahim (2019) evaluated the combined effects of CSIs *viz*., Nomolt (teflubenzuron); Ekio (novaluron) and Magic Smart (lufenuron) with EPNs *S. carpocapsae* and *H. bacteriophora* against*S.littoralis*. All tested IGRs caused low mortalities of EPNs. The combined efficacy of *S. carpocapsae* or *H. bacteriophora* with each of these IGRs, at LC_{25}, was effective for causing high mortality of *S. littoralis*. In Egypt, also, the compatibility of Egyptian strains of EPNs (*H. bacteriophora* (HP88) and *S. carpocapsae* (AT4) with lufenuron and its activity against the 4th instar larvae of *S. frugiperda* had been studied by El Roby *et al*. (2023). According to their results, all mixtures of lufenuron with EPNs have synergistic effects against 4th instar larvae except at the concentration LC_{25} was antagonist.

In contrast to the aforementioned results, results of some studies revealed an incompatibility of some EPN species with certain CSIs, such as cyromazine which did not exhibit synergistic interaction with *H. bacteriophora* Poinar "GPS1" for control of onion maggot *Delia antique* (Diptera: Anthomyiidae) (Yildrimand Hoy, 2003). Also, Zart *et al*. (2021) evaluated the performance of nine isolates of *H. amazonensis* and one of *H. indica* in mixtures with certain compounds against the mealybug *Dysmicoccus brevipes* (Hemiptera: Pseudococcidae). In the compatibility test, Curyom (lufenuron 550 EC) was the only one that reduced the infectivity (92% reduction) of the isolate NEPET11 (*H. amazonensis*) and, thus, it could be classified as a moderately toxic compound.

4. Interactions between EPNs and Fertilizers: Compatibility Or Incompatibility?

4.1. Agricultural Management Practices And Soil Amendments In Relation to EPNs - an Overview:

First and foremost, the addition of organic and inorganic soil amendments to improve soil fertility and plant growth is among the oldest agricultural practices (Kaya, 1990). Early, Georgis and Gaugler (1991) emphasized the reducing effects of some soil amendments on the efficacy of EPNs. In this context, it is important to shed some light on the fertilizers and amendments in the agricultural soil, the most suitable habitat in which

EPNs spend most of their life and have host-finding behavior. Some authors (Şahin and Susurluk, 2018; Bamel*et al*., 2020) reported that the occurrence, abundance, viability and reproduction of EPNs, as well as their virulence against soil-dwelling insect pests, can be remarkably affected by several factors including the soil physico-chemical properties. According to Kandji *et al*. (2001), the correlations between soil physico-chemical properties and EPNs play an important role in the distribution and biodiversity of EPNs' communities. As shown in the current literature, several studies have examined the negative effects of intensive soil management on EPN populations (Hummel *et al*., 2002; Campos-Herrera *et al*., 2008, 2010, 2014). Now, it is well known that different agronomic practices, such as irrigation, tillage and fertilization, have affected the abundance and insecticidal activities of EPNs (Susurluk, 2008; Hussaini, 2017). Therefore, the potential interaction of EPNs with soil amendments, whether synergistic or antagonistic, is a key factor for successful biological control using EPNs (Forschler *et. al*., 1990; Jaffuel *et al*., 2016).

Selected aspects should be highlighted in this context, since EPN virulence can be affected by many biotic and abiotic factors, under field conditions, including the soil microbiome (community of microorganisms and the used EPN species), cultivated plant genotypes, soil properties (texture, moisture, temperature, pH, organic matter content, *etc*.), and characters of the used fertilizer, such as its physical status, mineralization rate, nutrient content, and decomposition products (Zhao *et al*., 2014; Hussaini, 2017; Sahin and Susurluk, 2018). For instance, some of the fertilizer decomposition products may be directly toxic to EPNs; fertilizer application may induce biotic activity in terms of predation and parasitism on EPNs. In a biological process, such as mineralization, its rate may vary with soil moisture, temperature and aeration. Some or all of these factors may contribute to reducing EPN virulence (Shapiro-Ilan *et al*., 2006; Campos-Herrera *et al*., 2019; Bruno *et al*., 2020). Also, the use of fresh manure has been shown to detrimentally affect the survival and virulence of EPNs (Lawrence *et al*., 2006; Selvaraj and Annamalai, 2011). In addition, the soil pH alone does have a strong effect on the EPN activity however at pH values above 10, the EPN activity declines rapidly (Lacey and Kaya, 2007). In their study, Kawaka *et al*. (2014) found that the soil pH ranged from 3.5 to 4.9 and this is considered favorable for the survival of EPNs.

In addition, the application of various pesticides has been reported to exhibit direct toxic effects on EPNs (Alumai and Grewal, 2004). Also, herbicides and fungicides are poorly tolerated by EPNs and have toxic effects on their survival and virulence (Koppenhöfer and Grewal, 2005). For some details, see the previous section "Compatibility of EPNs with synthetic insecticides" in the present review. As previously mentioned, EPNs are affected by various abiotic soil properties which might be drastically altered by agricultural management practices and biotic factors, such as competitors and natural enemies (Stuart *et al*., 2006; Stuart *et al*., 2015; Lewis *et al*., 2015). Understanding these interactions is essential to reveal suitable measures to promote the potential of EPNs as biocontrol agents in a particular soil type (Jaffuel *et al*., 2016).

Generally, attributes of the used fertilizer (Bednarek and Gaugler,1997; Sahin and Susurluk, 2018), EPN species (Susurluk, 2008), and relevant settings (Shapiro *et al*., 1996; Shapiro *et al*., 1999; Hussaini, 2017) should be taken into consideration when assessing EPN efficacy for use in the biological control of insect pests (Rufai *et al*., 2020). With regard to organic and inorganic fertilizers, various studies investigated the effects of these additive compounds on the EPNs fitness (Bednarek and Gaugler, 1997; Shapiro *et al*., 1999; Hussaini, 2017). On the other hand, little research has been conducted to determine the effects of different fertilizers on the symbiotic bacteria of EPNs (Mullens *et al*., 1987).

4.2. Compatibility of EPNs with Organic Fertilizers:

To our knowledge, few studies have reported positive effects of organic soil management on the EPNs (Briar *et al*., 2007; Campos-Herrera *et al*., 2008, 2010). For example, some studies have determined a reduced survival of the EPN *S. carpocapsae* after mixing with fresh manure (Mullens *et al*., 1987) but enhanced survival in compost (Ishibashi and Kondo, 1986). These results were, to some extent, in agreement with the results of Shapiro *et al*. (1996) who recorded a reduction of the *S. carpocapsae* virulence against *G. mellonella* by urea and fresh manure in laboratory experiments. In the field experiments, however, only the fresh manure treatment reduced the EPN virulence. In both laboratory and field experiments, composted manure did not affect the EPN virulence. According to the results of the same authors, also, the effect of a fertilizer on *S. carpocapsae* virulence was more rapid in a soil of low content of organic matter than in a soil of rich organic matter.

On the other hand, Bednarek and Gaugler (1997) reported that the organic manure, used as fertilizer, may encourage EPNs establishment and recycling. More than two decades later, Bamel *et al*. (2020) determined the direct effects of soluble fertilizers on the EPN *H. indica*. Depending on their results, urea phosphate was found to be the most lethal, as compared to other fertilizers. There was a positive correlation between the concentration of fertilizer and mortality of IJs of the EPN *H. indica*. Also, the infectivity of *H. indica* decreased with the increase of incubation period from 1 to 3 and further to 5 days.

4.3. Compatibility of EPNs with Inorganic Fertilizers:

Currently, many investigators have paid attention to investigating the effects of inorganic fertilizers on different traits of EPNs. Bednarek and Gaugler (1997) assessed the impact of some inorganic and organic fertilizers on the infectivity, reproduction, and population dynamics of EPNs. They concluded that inorganic fertilizers were likely to be compatible with EPNs in tank mixes and should not reduce the pathogenicity of EPNs used for short-term control as biological control agents, but may interfere with attempts to use EPNs as inoculative agents for long-term control.

For some detail, the effect of calcium phosphate on survival, infectivity and penetration efficiency of the Egyptian strains HPS1, HPS2 and HPS3 of *Heterorhabditids* sp. was evaluated by Azazy *et al*. (2012), in Egypt, against larvae of *G. mellonella*. According to their results, calcium phosphate (at low concentrations of 0.2M and 2M) was less suppressive on the survival of the three EPN strains and did not affect their infectivity against *G. mellonella* (100% larval mortality), but medium concentrations affected the EPN infectivity. According to their results, also, calcium phosphate at three concentrations reduced the penetration efficiency of all EPN strains. Also, the direct effects of some inorganic fertilizers had been investigated by Şahin and Susurluk (2018), in Turkey, on the EPNs *S. feltiae* (Tur-S3) and *H. bacteriophora* (HBH). *S. feltiae* was more resistant to the tested inorganic fertilizers than *H. bacteriophora*. The diammonium phosphate (DAP), nitrogen phosphorus potassium (NPK) and nitrogen and phosphorus (NP**)** exhibited more adverse effects than the other fertilizers on both EPN species. These results agreed with those results of Susurluk (2008) who found that prolonged exposure to high concentrations of NPK inhibited the activities of *Steinernema* spp. and *Heterohabditis* spp.

In recent years, a study by Kolombar *et al*. (2020) revealed that mineral fertilizers(mineral additives) slightly reduced the vitality of IJs of different EPN species, while survival and viability of the IJs cultures of the EPNs increased during the use of solutions of ascorbic acid, B_1, B_6 or B_{12}. Thus, these authors recommended the use of these vitamin solutions for improving the viability of EPN preparations at the concentrations of 6–50, 25–50, 25–50 and 0.1–0.2 mg/mL respectively. In Egypt, Shehata *et al*. (2021) examined the effects of different inorganic fertilizers (such as ammonium sulfate, ammonium nitrate, calcium nitrate, ammonium phosphate, potassium sulfate, NPK, potassium nitrate)on the virulence of indigenous EPN*S.glaseri*. Based on their results, phosphorus fertilizers exhibited stronger reducing effects than others on the EPN virulence.

Except for phosphorus fertilizers, 1% fertilizer concentrations are compatible with *S. glaseri* in tank mixes for short-term (1–7 days) insect control but may affect long-term control. However, the effects of inorganic fertilizers varied according to their chemical composition, the EPN species exposed, and the duration of its exposure to the fertilizer (Guo *et al*., 2013; Sahin and Susurluk, 2018).

With respect to the symbiotic bacteria of EPNs, Downs *et al*. (2022) investigated the effects of various organic and inorganic fertilizers on the density of *Xenorhabdus nematophila* and *Photorhabdus luminescens* (symbiotically associated with EPNs *S. carpocapsae* and *H. bacteriophora*, respectively). They concluded that *P. luminescens* are generally more sensitive to fertilizers than *X. nematophila*. Moreover, those fertilizers containing high nitrogen content suppressed the bacterial densities more readily than those with lesser content. Also, bacterial symbionts exposed to inorganic (synthetic) fertilizers had greater population declines as well as greater mortality rates than those treated with organic amendments.

In summary, EPNs are affected by various abiotic soil properties which might be drastically altered by agricultural management practices and biotic factors, such as competitors and natural enemies. Different agronomic practices affect the abundance and insecticidal activities of EPNs. For example, tillage and herbicide applications may suppress the EPN abundance. Fertilizers may reduce the EPN population density and activity for several reasons, such as the direct toxic effects of fertilizers or their decomposition products EPNs; an increase in biotic activity as a result of fertilizer application may increase predation and parasitism on EPNs; or fertilizers may reduce EPN survival by modifying the soil-physical status. However, the effects of inorganic fertilizers varied according to their chemical composition, the innate characteristics of EPN species, and the duration of their exposure to the fertilizer.

Because the potential interaction of EPNs, whether antagonistic or synergistic, with soil amendments is a key factor for successful biological control use, the attributes of the used fertilizer, EPN species, and relevant settings should be taken into consideration when assessing the EPN efficacy for use in the biological control of insect pests. In other words, understanding these interactions is essential to reveal suitable ways to enhance the potential of EPNs as biocontrol agents in a particular soil type

5. EPN Tolerance and Susceptibility to Heavy Metals and Other Soil Chemical Pollutants:

5.1. Hazardous Heavy Metals and Soil Pollution to Biota - A General Outlook:

Firstly, heavy metals are common soil pollutants, *viz*., arsenic (As), cadmium (Cd), chromium (Cr), mercury (Hg), lead (Pb), copper (Cu), zinc (Zn), nickel (Ni). Carreira *et al*. (2004) reported that heavy metal contamination in the soil is caused by various types of metals, mainly Cu, Ni, Cd, Zn, Cr, and Pb. These pollutants are widely distributed and persist long-term in the soil environment (Ma *et al*., 2013). They are classified into the group of toxic elements, with very high degrees of risk for the environment (Kabata-Pendias and Brummer, 1992). Based on physical, physiological, and chemical properties, Pourret and Hursthouse (2019) classified the heavy metals into transition metals: such as Cr, manganese (Mn), iron (Fe), cobalt (Co), Ni, Cu, and molybdenum (Mo); post-transition metals: such as aluminum (Al), Zn, Cd, Hg, and Pb; alkaline earth metals: such as calcium (Ca), magnesium (Mg), beryllium (Be), and barium (Ba); alkali metals: such as lithium (Li), sodium (Na), potassium (K), and cesium (Cs); and metalloids, which are also referred to assemi-metals because of their metallic and non-metallic properties: such as boron (B), silicon (Si), As and antimony (Sb).

Although heavy metals naturally occur in the earth’s crust with large differences in concentrations, the pollution resulting from human activities has contributed to the high existence of heavy metals in the ecosystem (Rasmussen *et al*., 2007). Heavy metals and metalloids are agricultural soil contaminants, because if present at high levels, they can negatively affect crop productivity (Maksymiec, 2007; Shahid *et al*., 2015). Also, there is more accumulation of heavy metals in the areas where agricultural activities, such as fertilizing, are conducted than in natural areas (Campos-Herrera *et al*., 2010).

However, heavy metals like Pb, Cd, and Hg are biologically toxic, not only at high concentrations but also at low concentrations (Nyiramigisha *et al*., 2021). The increase of heavy metals concentrations in the soil results in toxic effects on the soil biota by affecting important microbial activities and reducing microorganism's density and distribution (Singh and Kalamdhad, 2011). These metals are contributors to metabolic abnormalities in organisms particularly the consumers of food from plants and other crops grown in contaminated soil (Bakshi *et al*., 2018). In addition, their accumulation in the soil has a negative influence on the physiological activities of plants, such as photosynthesis, gaseous exchange, and nutrient absorption which result in plant growth reduction and dry matter accumulation (Gebre and Debelie, 2015; Ozcan *et al*., 2016).

Once heavy metals have been introduced into the soil, they cannot be degraded either biologically or chemically and can persist in the environment for a long time, therefore, they cause serious environmental pollution and harmful effects on the ecosystem (Hoornweg and Bhada-Tata, 2012; Kasam *et al*., 2018). Many investigators have paid attention to soil contamination concerning the introduction of dangerous elements into the food chains through uptake by plants and thereby affecting food safety (Ozcan *et al*., 2016). From the physiological point of view, many heavy metals are included in coenzymes, active parts of vitamins, and respiratory dyes. They become if they enter biochemical reactions, which they normally do not take part in, and replace suitable substances (Jaworska *et al*., 1999). Moreover, heavy metals penetrate into mitochondria and cause interruptions in the process of gas exchange; they also influence the ability of reproduction. Together with food, an animal may receive some xenobiotic elements, like Cd and Pb, which do not take part in metabolism, they are very dangerous, but they are consumed and assimilated by the animal, but become toxic when their concentrations become more than the allowable level (Hopkin, 1994; Alengebawy *et al*., 2021). Recently, Abdur Rashid *et al*. (2023) provided a comprehensive review to evaluate several aspects in this context, such as the heavy metals and metalloids contamination in arable lands through agricultural practices, particularly due to chemical fertilizers, pesticides, livestock manures and compost, sewage-sludge-based biosolids, and irrigation.

5.2. Interactions Between EPNs and Heavy Metals:

In the world, several investigators have paid great attention to the interaction between EPNs and soil pollution with heavy metals and other pollutants (Korthals *et al*., 1996; Shukurov *et al*., 2005; Moreno and Navas, 2007; Pen-Mouratov *et al*., 2008).EPN species diversity has been influenced by soil pollution, including pollution with heavy metals. For example, it, Directly and indirectly, influences the abundance of EPN species, their diversity and biomass (Kamionek *et al*., 2011). In this context, Kawaka *et al*. (2014) determined the effects of selected soil chemical characteristics on the occurrence of EPNs under different land uses in Kenya. They concluded that soil fertility management practices and heavy metals influence the occurrence of EPNs and should be considered for their effective use as biological control agents.

As reported in the current literature, some heavy metals inhibit the EPN pathogenicity, while other heavy metal ions stimulate it (Pezowicz, 2004). On exposure to heavy metals, if EPNs do not respond directly by higher mortality, their infectivity and pathogenic abilities to hosts have decreased, which adversely affects their potential for pest control (Jaworska *et al*.,1997; Jaworska, 2014; Sun *et al*., 2016). Amounts of metals, such as Iron ($Fe2^+$), have been reported to have a weak vitalizing effect on the infectivity of EPNs with respect to caterpillars of *G.mellonella* (Jaworska *et al*., 1997). However, Campos-Herrera *et al*. (2008) showed that metals, such as Cr, Fe, Mo, Ni, Va, Cd, Zn and Li, negatively affect the virulence and infectivity of EPNs. As reported by some authors (Jaworska and Gorczyca,2002; Debojit*et al*., 2011), high levels of some heavy metals negatively affect the survival, virulence and infectivity of EPNs.

Kamionek *et al*. (2011) determined the influences of lead nitrate and cadmium nitrate on the EPN *S. feltiae* Filipjev infecting larvae of *G. mellonella*. Their results revealed various reducing effects of different concentrations of these metal compounds on the EPN vitality and IJs production inside the host body. A few years later, Jaworska (2014) evaluated the effect of magnesium sulphate on the reproduction of *S.feltiae* and the pathogenic abilities of its IJsliving in soil polluted with petrol, diesel oil and used engine oil. In the same regard, Ropek and Gospodarek (2022) evaluated the effect of soil pollution by petrol, diesel fuel and engine oil on the virulence of *S. feltiae*. Soil pollution with oil derivatives has a negative effect on *S. feltiae* ability to penetrate larvae of the mealworm beetle*Tenebriomollitor* (Coleoptera: Tenebrionidae). The mortality of *T. mollitor* caused by *S. feltiae* was a sufficient indicator of the progress of bioremediation of petroleum pollutants, such as diesel oil and engine oil.

5.3. EPNs and Non-Toxic Metal Ions:

Several elements are classified as essential mineral nutrients for plant growth and productivity. Examples include Cu, Zn, Fe, Mn, Mo, Ni, Mg, Ca, and B. At relatively low concentrations, these elements can enhance specific cellular processes in plants including ion homeostasis, photosynthesis, enzyme activities, respiration, nitrogen fixation, sugar metabolism, *etc*. (Shahid *et al*., 2015; Bashir *et al*., 2016; Tiwari and Lata, 2018). However, when accumulated at concentrations over the optimum, the same essential elements can adversely affect plant growth, development, and reproduction (Maksymiec, 2007; Shahid *et al*., 2015). Conversely, if the concentration declines under certain threshold levels, they also produce mineral deficiency symptoms in plants (Bashir *et al*., 2016).

With regard to the compatibility of EPNs with chemical elements, many chemical elements, such as Cu, Fe, Co, Se, Zn, occur in trace amounts in the living body and are essential for growth, development, and vitality. Because of their importance to the EPN vitality, essential chemical elements have received special attention from several nematologists(Nachev *et al*., 2013). Jaworska *et al*. (1997b) carried out some *in vitro* tests in the laboratory indicating the affected vitality and infectivity of EPNs in the presence of non-toxic metal ions. As shown by their results, also, Mn and Mgdid not affect thesurvivalofIJsofEPNs*S.carpocapsae*and*H.bacteriophora* but enhanced their infectivity against *G.mellonella*. Also, a slightly stimulated reproduction of *S. feltiae* by Mn was recorded by Jaworska and Gorczyca (2002). Also, the same authors showed the role of both Mn and Mg inneutralizing the negative effect of Pb on *S. feltiae* mortality.

In contrast, some authors (Jaworska and Gorczyca, 2009; Sun *et al*., 2016) reported reducing effects of Cd, Cr, Zn, Pb, and Cuonthe reproduction of *S.feltiae*, *S. carpocapsae*, and *H. bacteriophora*and reduced virulence against *G. mellonella*. However, the exact roles of Cd and Se in EPN biology are still unknown (Jaworska and Gorczyca, 2009).

For the improvement of EPNs, as effective bio-control agents, and a better understanding of the possible roles of non-toxicmetals in their physiology, Meligy (2018) studied the levels of ten elements in IJs of five Egyptian isolates of Steinernematidae and Heterorhabditidaefamilies. According to his results, Cu was the most abundant element in all EPN isolates. This result could be explained by the ability of EPNs, during their early stages inside the insect body, to collect and accumulate Cu from the surrounding Cu-rich insect haemolymph (Malik and Malik, 2009). Also, the abundance of Cu might be due to the

Cu accumulation in IJs by the symbiotic bacteria associated with EPNs (*Photorhabdus* of *Heterorhabditis* spp. and *Xenorhabdus* of *Steinernema* spp.), for which Cu is known to be an essential trace element (Kuzuya and Inouye, 2001; Watson *et al.*, 2010; Massaoud *et al.*, 2011). The uptake of *Photorhabdus* bacteria (associated with Heterorhabditidae)to Fe could also explain the detected high concentration of Fe ions in IJs and also explains their significantly higher concentration in EPNisolates related toHeterorhabditidaefamily than the concentration in isolates related to Steinernematidae family (Meligy, 2018). However, Jaworska *et al*. (1997a) mentioned that Fe and Cuions vitalized IJs of *H.bacteriophora*and promoted their mobility and pathogenic abilities against the insect host.

5.4. EPNs Are Good Bio-Indicators of The Environmental Pollutants:

In recent years,bio-indication has become an important tool for assessing the quality of soil environments. To unveil the real impact of pollutants on the environment, biological, not only physicochemical, methods should be used (Maurya *et al*., 2020).In this context, it is well known now that EPNs are natural enemies of many serious insects. Therefore, they have been increasingly used for the biological control of insect pests (Tomalak, 2006; Nouh and Adly, 2021; Patil *et al*., 2022). These EPNs are widely distributed, abundant and highly diverse, and play a key role in soil functioning (Van den Hoogen *et al*., 2019). They have been reported to respond differentially to xenobiotic substances (Bongers *et al*., 2001; De Nardo and Grewal, 2003; Jonker *et al*., 2004).

As reported by several authors (Bongers and Ferris, 1999; Neher, 2001; Bongers *et al*., 2001; Georgieva *et al*., 2002; Achazi, 2002; Hao *et al*., 2010), EPNs are considered the most promising candidates for bio-indication of soil status and assessing the disturbance of soil ecosystem, particularly in soils polluted with heavy metals.EPNs have been recognized as good bioindicators of soil fertility since the 1970s in both Europe (Zullini, 1976; Devi, 2020) and NewZealand (Yeates, 1979), and since the 1980s in the USA (Yeates and Coleman, 1982; Ingham *et al*., 1985; Freckman, 1988).In recent years, Khanum *et al*. (2021) reported that soil EPNs have advantages as bio-indicators because they have a beneficial role in the food web. EPNs, associated with their endosymbiotic bacteria, are probably the most studied bio-indicators of soil health and fertility because they have different beneficial ways to increase soil functions.

As previously mentioned, EPNs are also sensitive to oil derivatives, which affect their death rate and ability to penetrate the host insects (Ropek and Gondek, 2002; Ropek and Gospodarek, 2013). This property makes them candidates as indicators for this kind of pollution. Generally, pollution can induce tolerance in EPNs through a selection of tolerant strains within the population (Millward and Grant, 2000). In their study, Ekschmitt and Korthals (2006) analyzed whether different EPNs genera proved sensitive or tolerant toward heavy metals and organic pollutants. They discussed overlaps between EPNphysiological responses to heavy metals and organic pollutants, which may explain why EPNs can exhibit co-tolerance toward several contaminants. For more details about the importance of EPNs as bio-indicators of environmental status, see reviews of Devi (2020) and Khanum *et al*. (2021).

6. Compatibility of EPNs with Crude Plant Extracts And Isolated Phytochemicals:

6.1. Botanicals for the Insect Pest Control-Basic Information:

Prior to reviewing the interactions between EPNs and phytochemicals, it is important to shed some light on the phytochemicals produced by different plants and their uses for insect pest control. The practice of using plant extracts for pest control is not new; they have been used for at least two millennia when botanicals were considered important products for pest control in Ancient China, Egypt, Greece and India (Isman, 2006; Dougoud *et al*., 2019). Also, these natural materials were usually used, before the discovery of synthetic insecticides in the late 1930’s and early 1940’s (Isman, 1997).

As reported by several authors (Nakatani *et al*., 2001: Clemente *et al*., 2003; Isman, 2008; Lokesh *et al*., 2017), plants contain numerous active phytochemicals of broad-spectrum insecticidal activity. Therefore, they have gained the great attention of researchers all over the world because of their safety to humans and beneficial animals, less toxicity to other non-target organisms and biodegradability in the environment ecologically acceptable(Ghoneim *et al*., 2000; Silva *et al*., 2002; Omar *et al*., 2007; Rawi *et al*., 2011). Because botanicals are effective alternatives to synthetic insecticides, they are useful in many pest management programs (Matthews, 1999; Shekari *et al*., 2008; Dadang *et al*., 2009; Ebadollahi, 2013). In Egypt, as an example, a large body of research has been conducted to monitor the insecticidal activity of extracts of different plants and various phytochemicals against many insect pests (Ghoneim *et al*., 2002, 2007, 2009, 2022, 2023; Farag, 2002; Sadek, 2003, Hamadah *et al*., 2013).

Functionally, phytochemicals kill the target insect pest directly or disrupt its physiological processes (Thompson *et al*., 2000; Smagghe *et al*., 2003; Magierowicz *et al*., 2019). They can act as attractive, repellent, or toxic agents, as well as growth disrupting agents against insects (Khambay *et al*., 2002; Liang *et al*., 2003; Dubey *et al*., 2010; Céspedes *et al*., 2013; Ben Hamouda *et al*., 2015a, b, c; Senthil-Nathan, 2015; Ghoneim *et al*., 2020, 2021; Hamadah *et al*., 2021). It is more difficult for insect pests to develop resistance to phytochemicals (Isman, 2000; Isman and Akhtar, 2007).

Until now, there are more than 2000 plant species known to have insecticidal properties, where the Meliaceae, Asteraceae, Labiateae, Piperaceae and Annonaceae are most promising for pest control(Isman, 2006). Later on, Castillo-Sánchez *et al*. (2010) reviewed different plant extracts from the Annonaceae, Meliaceae and Solanaceae families and the compounds or mixtures of compounds obtained as well as their modes of action against insect pests. On the other hand, plants that have biological activity against insects contain secondary metabolites, some of which have been widely investigated (Salvadores *et al*., 2007; Chandra *et al*., 2008). Nowadays, these metabolites are no longer termed secondary, but rather specialized metabolites (Kortbeek *et al*., 2019). These metabolites are used for defense against herbivorous insects (Carpinella *et al*., 2002; Ahmad, 2007; Urzúa *et al*., 2011; Céspedes *et al*., 2013).

The currently available literature reported hundreds of compounds isolated and identified from tens of metabolites from various higher plants and reported as potent control agents against various insect pests(Carpinella *et al*., 2002; Koul, 2005; Simmonds, 2006). Among these metabolites are diterpenoids,triterpinoids, sesquiterpenoids, sesquiterpene lactones, flavonoids, quassins, quinines, alkaloids, limonoids, cucurbitacines, tannins, steroidal glycosides, steroidal saponins, steroids, phenylpropanoids, aromatic steroids and phenolics stand out (Urzúa *et al*., 2010a, b; Paul and Choudhury, 2016; Hikal *et al*., 2017). On the other hand, some authors (Lingathurai *et al*., 2011; Guzel *et al*., 2015)reported that among the plant metabolites with biological activities against insects, flavonoids, terpenoids, alkaloids, steroids and phenols stand out.

For detail, terpenes are a large and diverse class of natural compounds that are produced by many plant species, and they play an important role in the defense mechanisms of plants against herbivores, pathogens, and other stress factors (Hazir *et al*., 2003; Grewal *et al*., 2005; Gershenzon and Dudareva, 2007; Lacey and Georgis, 2012; Singh and Sharma, 2015; Boncan *et al*., 2020; Yüksel *et al*., 2022). They exhibit a broad spectrum of effects, ranging from toxicity to insects (Lee *et al*., 2003), fungi (Hammer *et al*., 2003), and bacteria (Friedman *et al*., 2002), to serve as feeding deterrents to mollusks (Frank *et al*., 2002), insects (Szczepanik *et al*., 2005), and mammals (Vourc'h*et al*., 2002). Terpenes have emerged as promising alternatives to synthetic insecticides in plant protection, with numerous commercial products developed for pest control and they are recognized as environmentally safe (Isman,2000; Koul *et al*., 2008; Seiber *et al*., 2014; Greff *et al*., 2023).

With regard to neem products, the neem tree, *Azadirachta indica*, is the most famous species in the family Meliaceae(order: Rutales). It has received much attention to developing alternatives to synthetic insecticides at least partly owing to the presence of limonoid triterpenes (Isman *et al*., 2002). Most research works have focused on azadirachtin, alimonoid from the seeds of *A. indica*. Neem seed extracts rich in azadirachtin (10-25%) act both as a potent antifeedant and insect growth regulator (Govindachari *et al*., 2000; Kraus, 2002). Debashri and Tamal (2012) reviewed several biopesticides based on the neem *A. indica*. The remarkable bioactivity exhibited by azadirachtin from *A. indica* led to the search for other natural insecticides in the closely related genus *Melia* such as *Melia azedarach*. Some of the limonoids isolated from the fruits of *M. azedarach* are meliantriol, melianone, melianol, meliacin (1-cinnamoyl melianone),meliacarpin and meliartenin (Carpinella *et al*., 2002).

In respect of plant growth regulators, Environmental Protection Agency defined the plant growth regulator (PGR)as "any substance or mixtures of substances intended, through physiological action, to promote or retard the rate of growth or maturation or otherwise alter the behavior of plants (Yau, 2011; Mahajan, 2015). Although these phytochemicals affect the physiological activity of plants, many PGRs appear to exhibit adverse effects on the survival, biology, physiology, biochemistry and behavior of herbivorous insects (Kaur *et al*., 2016; Abo Elsoud*et al*., 2021 a, b; Ghoneim *et al*., 2022, 2023; Hamadah *et al*., 2022). In the last four decades, many authors (Kaur and Rup, 2002; Ahmad *et al*., 2003; Silva *et al*., 2003; Kaur and Rup, 2003; Gupta *et al*., 2009; Bhatnagar, 2010; Uçkan *et al*., 2011a, b, 2014, 2015; Altuntaş, 2015; Abdellaoui *et al*., 2015) suggested that the PGRscan be used as alternative to the synthetic insecticides for controlling the economically serious insect pests. In addition, synthetic PGRs mimic the authentic PGRsand are marketed specifically for the purpose of stimulation or retardation of plant growth and development. They are, also, used for reduction of the insect pest infestation on crop plants (Gupta *et al*., 2009; Memon *et al*., 2011; Ali *et al*., 2012).

In summary, plant-derived substances, natural plant products and bio-insecticides have recently become of great interest owing to their versatile applications for the protection of economically important crops due to their low mammalian and vertebrate toxicity, as well as low persistence and no undesirable effects on animals and human beings (Raja *et al*., 2001; Meena *et al*., 2006). Natural products, such as plant extracts and products, form promising nonconventional pesticides against destructive pests for crops and health. Neem products, as an example, were considered effective insect growth regulators (Hashim and Devi, 2003) and toxicants (Saxena *et al*., 1989; Baris *et al*., 2006). Because of the multiple sites of action through which the plant materials can act, the probability of developing a resistant population is very low (Isman, 2006). Some authors used the term "phytopesticides" or "botanical insecticides" to describe many phytochemical compounds that exhibit various mechanisms of action; likewise, they are of lesser risk to human health compared to the available synthetic insecticides (Malahlela *et al*., 2021; Idris *et al*., 2022). They degrade rapidly in air and moisture and are readily broken down by detoxification enzymes. This is very important because rapid breakdown means less persistence in the environment and reduced risks to non-target creatures (Isman, 2008).

6.2. Compatibility of EPNs with Crude Plant Extracts:

Crude plant extracts are considered one of the most important control agents against insect pests because they are less hazardous to non-target organisms, environmentally safe, biodegradable, cheap, and effective, as well as they may have different modes of action and inadequate development in pests (Senthil-Nathan *et al*., 2009; Mansour *et al*., 2012; Cantrell *et al*., 2012; Kabir *et al*., 2013). The compatible relationship between plant extracts and the EPNs may lead to improved pest control in agricultural systems (Oso *et al*., 2021).

Based on the available literature, there are some studies focusing on the interaction between EPNs and plant extracts. For example, Kulkarni *et al*. (2013) found that a combination of the extracts of jatropha, pongamia, and custard apple, allowed survival of only 42.40% IJs of EPN *S. carpocapsae* after exposure to the highest concentration (0.3%), while the lowest concentration (0.05%) allowed more survival (84.0%). In another study, the effects of aqueous extracts of green waste compost, dry leaf litters of the common walnut (*Juglans regia*)(Family: Juglandaceae) and Norway maple (*Acer platanoides*) (Family: Sapindaceae)were determined on IJs of EPNs *H. bacteriophora*, *S. carpocapsae, S. feltiae*, and *S. kraussei* (Petrikovszki *et al*., 2019). According to the results of this study, green waste compost extracts caused quite low or no mortality of all EPN species. Mortality caused by the Norway maple leaf litter extract (concentration 5%) was moderate (34.6%) in the case of *S. carpocapsae* IJs, the highest concentration(5%) of the common walnut leaf litter extract caused 100% mortality in all EPN species. As a conclusion, green waste compost mulch seemed to be more compatible with EPN species than common walnut or Norway maple leaf litter mulch.

Quiescence (or dormancy) of EPNs normally is triggered by adverse environmental conditions (Barrett, 1991). During this state of dormancy, the metabolism of EPNs is strongly reduced allowing them to conserve energy, which can significantly prolong their lifespan and infectiousness (Hiltpold *et al*., 2014). Quiescence is finished when the conditions turn more favorable. Quiescence also can be chemically triggered, such as with compounds in exudates of root caps of certain plants (Hubbard *et al*., 2005; Zhao *et al*., 2000). Hiltpold *et al*. (2014) showed that exposure to pea root cap exudates conserves the EPN motility and infectivity. In this respect, also, Jaffuel *et al*. (2015) carried out a study to assess extracts from pea (*Pisum sativum*) (Family: Fabaceae) and maize (*Zea mays*)(Family: Poaceae) roots for induction of the quiescence in the EPN*H megidis*. Based on their results, IJs exposed to these extracts readily recovered from their quiescent state.

Pulavarty *et al*. (2020) evaluated the effect of Alltech®(an organic product consisting of a blend of fermentation and plant extracts with micronutrients) on EPNs (*S. feltiae* (SB12(1), a wild enviroCORE strain and a commercial form e-NEMA), *S. carpocapsae* (e-NEMA), and *H. bacteriophora*) in the greenhouse of tomato plants. They found no significant difference in the survival of IJs with 4% Alltech® compared to the control. A twofold reduction in survival was observed after exposure of EPN to 7% Alltech®. Therefore, Alltech® showed potential as a sustainable soil health alternative causing no harm to EPNsat concentrations below 4%. According to Oso *et al*. (2021), the compatibility of some extracts of the medicinal plants *Alepidea amatymbica* (Family: Apiaceae) and *Elephantorrhiza elephantina* (Family: Fabaceae) was assessed with five locally isolated EPN strains, *Steinernema* (*S. khoisanae*, *S. biddulphi* and *S. innovationi*) and *Heterorhabditis* (*H. bacteriophora* and *Heterorhabditis* sp. SGI 244). This study has shown that the corm and root extracts of *A. amatymbica* and *E. elephantina* are compatible with EPN strains and enhanced their virulence against the mealworm beetle *Tenebrio molitor* (Coleoptera: Tenebrionidae) after 72 h post-exposure.

On the contrary, the available literature contains some studies revealing the incompatibility of certain EPNs with crude extracts of a number of plants, since survival, viability, or/and infectivity of EPNs against insect pests may be adversely affected by these extracts. For example, the toxic effect of tannin-rich plant extracts was recorded in the case of *H. bacteriophora* (Glazer *et al*., 2015). According to results obtained by Rohde *et al*. (2013), aqueous extracts of chinaberry fruits (*Melia azedarach*)(Family: Meliaceae), common rue leaves (*Ruta graveolens*)(Family: Rutaceae), ginger (*Zingiber* *officinale*)(Family:Zingiberaceae) and garlic (*Allium sativum*) (Family: Amaryllidaceae) reduced the viability and infectivity of *S. carpocapsae* against larvae of *C. capitata* and EPN became incompatible after 120 h of exposure.

In a study of Shamseldean *et al*. (2013), the compatibility of the EPNs*H. indica* and *H. bacteriophora* with plant oils (like mint oil, camphor oil)or plant extracts(like extracts of *Dodonaea viscose,* family: Sapindaceae, and *Euphorbia cotimfabia*, family: Euphorbiaceae) was investigated against grasshopper*Heteracrirlittoralis* (Orthoptera: Acrididae). Based on their results, IJs of EPNs were negatively affected by the presence of plant oils and extracts. Also, the grasshopper was susceptible to EPN species, either alone or combined with plant oils and plant extracts. In another study, Santhi *et al*. (2017) recorded inhibitory effects of ethanolic extracts of *Inula viscose* (Family: Asteraceae), *Salix alba* (Family: Salicaceae) and *Quercus calliprinos* (Family: Fagaceae)on the developmental stages(eggs and young infective juveniles, IJs) of EPN *H. bacteriophora*.

The oil extracted from the herb *Ferulaasa foetida* (ASF)(Family: Apiaceae) has been used as an insect repellent against thrips, feeding deterrent and as an insect oviposition deterrent (Shakeri, 2004; Noonari *et al*., 2016; Shaik *et al*., 2017). Co-examining the relationship between ASF and EPNsmay be the most effective method for assessing the virulence and pathogenicity of EPNsagainst insect pests. Most of the ASF/nematode co-interaction research has been conducted on plant or alimentary parasite nematodes, with no reports on EPNs (Farhadi *et al*., 2016; Tavassoli *et al*., 2018). Recently, Abdul Shaik and Mishra (2023) carried out a study to elucidate the metabolic factors underlying the co-interaction of ASF with the EPN*S. carpocapsae* and their symbiotic bacteria, *Xenorhabdus nematophila*, revealing their virulence in the host European firebug *Pyrrhocoris apterus* (Hemiptera: Pyrrhocoridae). The *S. carpocapsae* pre-treated with 100 mg of ASF caused 24–91.4% *P. apterus*'s mortality during a period of 24 to 72 h. The topical application of ASF acted as a deterrent to *S. carpocapsae*, inhibiting the host invasion to 70% and delaying infectivity with 30% mortality for 168 h. In this study, the modulation of immunity in *P. apterus*, during such co-interactions, was also studied. EPN/ASF combination showed an immunomodulatory effect in *P. apterus*.

6.3. Compatibility of EPNs with Plant-Derived Compounds:

Several authors (Bedding, 2006; Laramliana and Yadav, 2008: Kulkarni *et al*., 2013; Lacy *et al*., 2015; Anes and Ganguly, 2016; Devi, 2022) reported that the combination of plant-derived products with EPNs can provide a new good commercial formulation for efficient pest control. As clearly shown in the current literature, interactions between EPNs and botanicals have been investigated by several studies showing tolerance, lethal or sub-lethal effects on survival and virulence, or synergistic effects on IJsof different species around the world (Hussaini *et al*.,2001; Sankaranarayanan, *et al*., 2006; Laznik, *et al*., 2012; Paunikar, 2014; Raheel *et al*., 2017). In other words, the compatibility varies with the EPN species, strain, botanical formulation, application dose and other factors (Koppenhoffer and Grewal, 2005). It may be important to mention that terpenes, such as limonene, pinene, caryophyllene, and pregeijerene, represent an important component of the EPN capability for finding an available host. Not all EPN species respond equally to terpenes because a terpene may be attractive to one EPN species and repellent to another, which could explain different susceptibility levels when two species are exposed to a terpene (Willett *et al*., 2015).

EPNs in Combination with Neem:

A comprehensive study by Halder *et al*. (2013) showed that a combination of neem oil®(Azadirachtin and other compounds)with entomopathogens was very successful against insect pests, particularly vegetable-sucking pests. Otherstudies have shown that neem oil® does not affect the survival, virulence, or infectivity of EPNs when combined together (Piggott *et al*., 2000). The compatibility of neem oil®tovarious EPN species was reported by many studies, such as two species of *Steinernema* and three species of *Heterorhabditis* (Hussaini *et al*., 2001), *S.carpocapsae* (Koppenhofer and Grewal, 2005) as well as *S. feltiae, S. asiaticum, H. bacteriophora* and *H. indica* (Raheel *et al*., 2017). According to Head *et al*. (2000), direct exposure of *S. feltiae* to neem oil® resulted in negligible effects on EPN survival. The soap surfactant in commercial neem products was found to cause low mortality (23-25%) of *S. feltiae* (Krishnayya and Grewal, 2002). A study of a combination of neem with two strains of *S. glaseri*, four strains/isolates of *H. bacteriophora* and an undescribed *Heterorhabditis* species from Korea was conducted against different species of white grubs (Coleoptera: Scarabaeidae). Results showed that their combination was better than the use of EPN alone (Koppernhoofer and Fuzy, 2003).

Also, the dual attack by EPNs combined with neem on the pest could have brought about the synergistic effect which resulted in the population reduction of the tomato leaf miner *Tuta absoluta* (Lepidoptera; Gelechiidae)(LaznicandTrdan, 2013). Also, EPN species, combined with neem pellets, were reported with additive effects on western flower thrips *Frankliniella occidentalis* (Thysanoptera: Thripidae)(Otieno *et al*., 2015).In another study, Nitjarunkul *et al*. (2015) found that the survival rate of *S. carpocapsae,* combined with neem, was more than 94.5%, but its virulence was decreased by longer soaking periods of *G. Mellonella* larvae. As shown by the results of Sinhouenon *et al*. (2019) on *P. xylostella* in northern Benin, the neem oil®displayed negligible effects on the survival of EPNs *Steinernema* sp. 83a and *Heterorhabditis sonorensis* KF723827. In addition, Paunikar and Kulkarni (2020) evaluated the compatibility of IJs of *S. dharanaii* (TFRIEPN-15) with neem oil®. Their results indicated no detrimental effect on the survival, infectivity and progeny production of *S. dharanaii,* which was exposed to the recommended lower or highest concentration of neem oil.

EPNs in Combination with Isolated Azadirachtin:

As previously mentioned, Azadirachtin(a tetranortriterpenoid derived from the neem seed of the Indian neem tree *Azadirachta indica* A. Juss, Meliaceae, Azt) is the most important neem product. TheAzt was reported to cause no harm to the survival or infectivity of EPN *S.carpocapsae* strain All (Yan *et al*., 2012) and other EPN species (Yan *et al*., 2012). Research conducted by Laznic and Trdan(2013) on the compatibility of Azt with EPNs revealed that the mortality rates for IJs were comparable with the control (water only) treatment. Similar results were previously obtained by Grewal et al. (1998) who showed that *S. feltia*e was compatible with Azt. Also, these results were in agreement with the results recorded by Ali *et al*. (2012) about the compatibility of EPNs with Azt at lower doses and short-term exposure.

In Egypt, Mahmoud *et al*. (2016) carried out some compatibility tests for *S. carpocapsae* and *H.bacteriophora* with Azt. Their results recorded greater efficacy against larvae of the black cutworm *Agrotis ipsilon* when EPNs were combined with, causing over 90% larval mortality. In Egypt, also, AskaryandAhmad(2020) conducted some compatibility tests for EPN *H. pakistanensis* with Azt under field conditions. Based on their results, *H. pakistanensis* (3.0 lakh IJs/m^2) +Azt (0.25%) caused 76.22% larval mortality of *P. brassica*. The cumulative mean survival of *H. pakistanensis* IJs recorded the highest (77.5%) in the combination of 100 IJs +Azt (0.25%). In Pakistan, Raheel *et al*. (2017) studied the compatibility of *S. feltiae, S. asiaticum, H.bacteriophora* and *H. indica,* with Azt against *G. Mellonella* larvae. They found that Azt proved to be compatible with all EPNs species. A few years later, a combination of Azt with the Turkish EPN isolates (*H. bacteriophora* FLH-4H, *S. carpocapsae* KCS-4S and *S. feltiae* KMP-9S) resulted in 70 - 95% larval mortality of *G. mellonella* under laboratory conditions (Yüksel and Canhilal, 2020). In contrast, the compatibility tests conducted by Jean-Baptiste *et al*. (2021) using *H. bacteriophora* HB and

S. brazilense (IBCB- n06) for the control of *C. capitata* revealed that Azt negatively affected the IJs of both EPN species. However, several studies with *Heterorhabditis* spp. and *Steinernema* spp. demonstrated their compatibility with Azt (Andaló *et al*., 2004; Radova, 2011; Yan *et al*., 2012; Laznik and Trdan, 2014; Chavan *et al*., 2018).

EPNs in Combination with some Azt-Based Products:

Since the isolation and identification of Azt from neem seed kernel and carrying out some bioassay tests against various insects and other animals, growing attention has been given to this product. Many companies in India (the origin) and other countries around the world paid great interest in formulating dozens of commercial products (with different concentrations of the active ingredient) under various trade names, such as NeemGuard, BioNeem, NeemAzal, Neemix, Nimor, Neemgold®, Nimbecidine®, *etc*. Some Azt-based products(NeemAzal T 5% and Neemix 4.5%) and the EPN*S.feltiae* were evaluated for controlling the peach fruit fly *Bactrocera zonata* (Diptera: Tephritidae). The combined use of these products, especially NeemAzal T 5%, with *S. feltiae* may offer an integrated approach to increase the efficacy of EPN to control *B. zonata*, (Mahmoud, 2007). Meyer *et al*. (2012) determined the effects of NeemAzal-U on the EPN*H. bacteriophora*. The number of IJs produced per *G. mellonella* larva was not influenced by NeemAzal-U treatments of IJs used for host infection. Against larvae of *A. ipsilon*, Mahmoud *et al*. (2016) assessed the combinations of EPNs *S. carpocapsae* and *H. bacteriophora* (at 80 IJs concentration) with Neemazal and neemix and recorded an induction of the EPNs efficacies to cause significantly increased larval mortality rates under the laboratory or greenhouse conditions. Therefore, they recommended the use of a mixture of Azt-based products + EPNs to achieve an efficient control of *A. ipsilon.*

Concerning the EPN computability with Neemgold®, Kulkarni *et al*. (2013) tested this product against EPN *S. carpocapsae*. Based on their results, the highest concentration (2.00%) allowed 69.60% survival up to 72 h, followed by 80.80% at the concentration of 1.5%, then 87.20% and 92.40% survival at a concentration of 1.00% and the lowest tested concentration (0.5%). Moreover, Neemgold® was reported to exhibit no detrimental effect on the survival, infectivity and progeny production of EPN *S. dharanaii*, which was exposed to the recommended lower or highest concentration of this product (Paunikar and Kulkarni, 2020). Some years later, Devi (2022) conducted a laboratory study to evaluate the compatibility of *H.bacteriophora* with Nimbecidineagainst*A.ipsilon*. His data showed that the survival rate of EPN exposed to Nimbecidine was 53% but its virulence against insect larvae ranged from 60 % to 70% mortality. Also, the penetration rate of IJs of *H. bacteriophora* in larvae reached 55.5% when exposed to 0.125% of Nimbecidine. Also, a combination of EPNs withNimor took 48h to cause 100% larval mortality of *G. mellonella* (Sankar *et al*., 2009). On the contrary, very few studies indicated the incompatibility of some EPN species with some Azt-based products. In a study, Meyer *et al*. (2012) found that NeemAzal-U caused remarkable mortality of *H. bacteriophora* but the virulence was not affected.

EPN in Combination with Botanicals Other Than Neem Products:

Limited knowledge exists in the current literature on the assessment of EPN combination with botanical compounds other than neem products. Derisom® EC is a bioacaricide/bioinsecticide based on the botanical extract of *Pongamia glabra*/ *Pongamia pinnata* (Karanj tree). Derisom® EC contains Karanjin as the active ingredient. Paunikar and Kulkarni (2020) evaluated the compatibility of IJs of *S. dharanaii* with Derisom®. The results indicated no detrimental effect on the survival, infectivity and progeny production of EPN, which were exposed to the recommended lower or highest concentration of this product.

In contrast, Santhi *et al*. (2019) examined the effects of some phenolic compounds (plant secondary metabolites) on the developmental stages of *H. bacteriophora*. They recorded the antagonistic effects of these compounds on EPN. The ability of EPN to tolerate phenolic compounds was stage-dependent, with early growth stages exhibiting less resilience than later growth stages. The EPN was able to survive in the presence of medium and low concentrations of all tested compounds, but very few of those treatments allowed for reproduction beyond the IJ stage and, at low concentrations. In a recent study, Kotsinis *et al*. (2023) evaluated the toxic effects of four terpenoids, thymol, carvacrol, eugenol, and geraniol, on *S. feltiae, S. carpocapsae, H. bacteriophora* and *H. indica* and their virulence against 4th instar larvae of *G. mellonella*. All terpenoids showed toxic activities against at least two of EPN species, and carvacrol was the most potent toxic and *H. bacteriophora*was the highest sensitive EPN. In their conclusion, terpenoids such as thymol, carvacrol, and eugenol, used commonly for pest control, should not be combined with *H. indica* and *H. bacteriophora* but could be combined with *S. feltiae* and *S. carpocapsae*.

EPN in Combination with Plant Growth Regulators(PGRs):

The current literature contains very limited results concerning the effects of PGRs on EPN survival, viability and infectivity.De Nardo and Grewal (2003) assessed the compatibility of EPN *S. feltiae* Filipjev with three PGRs, ancymidol (A-Rest), paclobutrazol (Bonzi), and uniconazole-P (Sumagic). The EPN was compatible with no loss in viability and infectivity up to 24 h of exposure. The viability of *S. feltiae* was more than 80% in all the products even after 72 h of exposure. Ozomite® is a natural product mined from an ancient mineral deposit in Utah (USA) that typically contains over 70 minerals and trace elements. It is used internationally as a feed additive and a soil re-mineralizer for plants. Paunikar and Kulkarni (2020) evaluated the compatibility of IJs of *S. dharanaii* with Ozomite®. The results indicated no detrimental effect on the survival, infectivity and progeny production of EPN, which were exposed to the recommended lower or highest concentration of this product.

Summary Points:

* Entomopathogenic nematodes (EPNs) are biocontrol agents against a wide variety of insect pests in the world for their characteristics of infectivity and compatibility with different control measures.

***** Several environmental factors directly influence EPN populations in the soil, such as humidity and temperature, as well as environmental extremes or the resistance of certain insect pests to EPN penetration. Under these circumstances, EPNs cannot exhibit high virulence on the targeted insect pests, therefore, they should be applied in combination with some compatible agrochemicals to enhance the control efficacy, with greater cost reduction in application time required.

* It should be kept in mind that the main goal of this strategy is the enhancement of EPN effectiveness for more efficient control of certain insect pests on the plants. In addition, this strategy has been applied to provide an understanding of how the naturally occurring EPN in soils can be better preserved in agroecosystems.

* In this context, many studies have found the infective juveniles (IJs) of EPNsare tolerant to short exposures (2-6 h) of many insecticides, fungicides and herbicides and therefore EPNs can be tank-mixed and applied together with these compounds.

* With regard to chemical insecticides, there has been increasing evidence that the combinations of EPNs with them represent a strategy to provide more effective pest control, particularly when both agents interact synergistically. Also, many EPNs belonging to the families Steinernematidae and Heterorhabditidae have been found to survive under exposure to different chemical pesticides.

* Some challenges should be taken into account since some insecticides did not interact with some EPN species while other insecticides enhanced the EPN efficacy (synergistic

interaction). Also, some studies indicated the detrimental impacts of some insecticides on the EPN efficiency, in terms of infectivity and survival, against several insect pests (antagonistic interaction).

* With respect to the insecticide categories, many studies worldwide indicated the compatibility of different EPNs with various kinds of organophosphates, while some studies reported the high toxicity of some insecticides of this class to survival of some EPNs or at least incompatibility with each other. The reported results of interactions between some EPN species and insecticides of other classes were almost similar to these obtained results.

* The majority of studies investigating the influence of herbicides on EPNs indicated that they have no drastic effects on different EPNs that were compatible with these agrochemicals. On the other hand, few studies have reported the incompatibility of certain EPNs with some herbicides. Some reported studies indicated almost similar results on EPNs with fungicides.

* Time of exposure is avery important factor for efficient EPN/insecticide combination because some studies revealed that the combination of chemical insecticides with *S. carpocapsae* and *H. indica* after 48 h of exposure have additive or synergistic effects on the targeted insect pest. By increasing the exposure time to 96 h, the interactions of EPNs and insecticides turned antagonistic and can reduce the EPN viability and infectivity.

* A great effort has been exerted in the world to handle the aforementioned challenges, since the extent to which EPNs interact with chemical pesticides depends on a number of factors, including EPN species, rates and timing of application, developmental stage of the targeted pest, exposure method and the environmental complexity in which the interaction takes place. Furthermore, the life stage of the targeted insect interferes with the compatibility of EPN with insecticides.

* Insect growth regulators (IGRs) have been used for insect pest control as an effective alternative to synthetic insecticides. Based on the specific mode of action, IGRs had been categorized into three categories: (i) juvenile hormone analogues, JHAs, also called Juvenoids), (ii) Ecdysteroid agonists and (iii) Chitin synthesis inhibitors (CSIs) or moult inhibitors.

* Little studies examined the compatibility of EPNs with juvenoid compounds. Results of some studies revealed compatibility of certain EPNs with some juvenoids while other studies recorded incompatibility and drastic effects of some juvenoids on the survival and viability of EPNs. To a great extent, similar results had been obtained for the combinations of EPNs with other IGR categories, ecdysteroids and chitin synthesis inhibitors.

* Naturally, EPNs are affected by various abiotic soil properties which may be drastically altered by agricultural management practices and biotic factors, such as competitors and natural enemies. Different agronomic practices affect the abundance and insecticidal activities of EPNs. For example, some organic fertilizers may reduce the EPN population density and activity. However, the effects of inorganic fertilizers on EPNs varied according to their chemical composition, the innate characteristics of EPN species, and the duration of their exposure to the fertilizer.

* Because the potential interaction of EPNs, whether antagonistic or synergistic, with soil amendments is a key factor for successful biological control use, the attributes of the used fertilizer, EPN species, and relevant settings should be taken into consideration when assessing the EPN efficacy for use in the biological control of insect pests.

* Several investigators have paid great attention to the interaction between EPNs and soil pollution with heavy metals and other pollutants. Some heavy metals were reported to inhibit the EPN pathogenicity, while other heavy metal ions stimulate it. On exposure to heavy metals, if EPNs do not respond directly by higher mortality, their infectivity and pathogenic abilities to hosts have decreased, which adversely affects their potential forpest control.

* Also, soil pollution by petrol, diesel fuel and engine oil negatively affects the virulence of some EPN species. Some authors mentioned that some non-toxic metal ions vitalized IJs of EPN and enhanced their mobility and pathogenic abilities against the insect host.

* Because EPNs play a key role in the soil functioning since they respond differentially to xenobiotic substances. EPNs, associated with their endosymbiotic bacteria, are considered the most promising candidates for the bio-indication of soil state and assessing the disturbance of soil ecosystem, particularly in soils polluted with heavy metals.

* Several studies concluded that the combination of plant-derived products with EPNs can provide a new good commercial formulation for efficient pest control. The interactions between EPNs and botanicals have been widely investigated and showed EPN tolerance or lethal effects of botanicals on their survival and virulence. Various plant-derived products were assessed in this area of research, such as neem, neem oil®, Azadirachtin and Azadirachtin-based products.

* In respect of botanical compounds other than neem products, very few studies have been conducted to assess the EPN computability with some compounds. Diverse results were obtained with the prevalence of antagonistic interactions. In addition, some EPN species were found compatible with a few plant growth regulators. However, such research can be considered still at the beginning stage. In addition, the compatible relationship between plant extracts and EPNs may lead to improved pest control in agricultural systems. Many studies in this area of research demonstrated diverse results.

* Finally, compatibility varies with the EPN species, strain, botanical formulation, applications dose and other factors

Conclusions and Future Prospective:

EPNs are biocontrol agents against various insect pests for their properties of infectivity and compatibility with different control agents. Under certain circumstances, they fail to exhibit high virulence on the insect pests; therefore, they should be applied in combination with some other control agents such as agrochemicals. Thus, the main goal of this strategy is the enhancement of EPN effectiveness for more efficient control. As clearly shown in the present review, the infective juveniles (IJs) of EPNsare tolerant to short exposures (2-6 h) of many insecticides, fungicides and herbicides and therefore EPNs can be tank-mixed and applied together with these compounds. Many EPN species belonging to the families Steinernematidae and Heterorhabditidae have been found to survive under exposure to many chemicals and pesticides of different classes. The majority of studies investigating the influences of herbicides and fungicides on EPNs indicated that they have no drastic effects on the survival, viability and infectivity of different EPNs. Also, research results revealed compatibility of certain EPNs with some insect growth regulators, fertilizers and phytochemicals, while few kinds of these agrochemicals have been found incompatible with EPNs.

In conclusion, the combination of EPNs with compatible agrochemicals is a promising approachto the pest control strategy. It has many advantages, such as reducing the dependence of farmers on synthetic insecticides alone.EPNs may be combined with various compatible agrochemicals with additive, or preferably synergistic, effects on pest mortality. For convenience, EPNs may also be tank-mixed with some compatible agrochemicals that are combined in the tank of the application tool, thus increasing the chances of interactions of both control agents. In this context, also, the exposure period should also be taken into consideration, because some authors reported that the exposure of EPNs to agrochemicals for a prolonged exposure period may turn their interaction to antagonistic in the meaning of low control efficiency against the targeted insect due to reduction ofEPN viability and infectivity.

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