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Review Article

Unraveling the Biology of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and its Biocontrol Potential Using Entomopathogenic Nematodes: A Review

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ABSTRACT

The fall armyworm (FAW), *Spodoptera frugiperda*, is a polyphagous pest that infest various plants. This highly invasive pest is native to the American continent and has spread rapidly over 100 countries worldwide. Its rapid spread and ability to cause severe damage to various crops, especially maize, pose a significant threat to food security, particularly in developing countries. Curative control using chemical insecticides is the primary choice in most countries, especially in Africa and Asia. However, dependence on chemical insecticides can have adverse effects on the environment and humans and can lead to the development of resistance to these pests. Therefore, various efforts have been made to develop effective, low-risk, and cost-efficient biocontrol measures. Entomopathogenic nematodes (EPNs) are a viable and potential choice for the biological control of this pest. This review compiles information on FAW, EPNs, and their developmental stages, focusing specifically on the pathogenicity of EPNs against FAW. This contributes to Integrated Pest Management (IPM) strategies addressing FAW infestations, which have caused severe maize crop losses in Malaysia since their detection in 2019. The potential for locally adapted EPN formulations tailored to Malaysia's climate ensures their practical application in the field.

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INTRODUCTION

The fall armyworm (FAW), *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae), is an invasive pest threatening global crop production systems. This pest can cause up to a 70% reduction in maize yield when crops are attacked early (Hruska, 2019). FAW infestations cause significant damage to other crops, such as cotton, rice, soybeans, tomatoes, potatoes, onions, beans, cabbages, sorghum, and a few pasture grass species (Day et al., 2017). *Spodoptera frugiperda* was first reported in Malaysia in 2019 (International Plant Protection Convention [IPPC], 2019; Jamil, Saranum, Saleh-Hudin et al., 2021). Since then, FAW infestations have caused severe damage, with 50%–100% crop loss in maize fields in Malaysia (Department of Agriculture [DOA], 2021; Jamil, Saranum, Mat et al., 2021).

Various preventive and curative approaches are being implemented to combat FAW attacks on maize crops, particularly regular monitoring, pheromone traps, ultraviolet (UV) light traps, agro-ecological methods, and the application of chemical and biopesticides (DOA, 2021). Curative control using chemical insecticides remains the primary choice for farmers. Reliance on chemical insecticides can adversely affect the environment and humans and increase the risk of FAW developing resistance to these chemicals (Guo et al., 2020). Entomopathogenic nematodes (EPNs) function similarly to entomopathogenic fungi and bacteria in reducing or replacing chemical insecticides (Cuthbertson & Audsley, 2016). Several studies have evaluated the pathogenicity of EPNs as potential biological control agents against FAW in laboratory and field environments. Therefore, this manuscript discusses the biology of FAW and EPNs pathogenicity against it.

TAXONOMY, ORIGIN, AND DISTRIBUTION OF THE FALL ARMYWORM (FAW), SPODOPTERA FRUGIPERDA

The fall armyworm (FAW) was initially named *Phalaena frugiperda* by Smith and Abbot in 1797. It was later known as *Laphygma frugiperda* (Luginbill, 1928) and, since 1958, has been referred to as *Spodoptera frugiperda* (European and Mediterranean Plant Protection Organization [EPPO], 2024). There are two strains of *S. frugiperda*: corn and rice (Food and Agriculture Organization of the United Nations & Plant Protection Division [FAO & PPD], 2020). Both strains have similar morphology but differ in pheromone composition, mating behaviors, and host plant selection (Dumas et al., 2015; FAO & PPD, 2020). The corn strain of *S. frugiperda* prefers maize, cotton, and sorghum as host plants, whereas the rice strain prefers rice and pasture grasses (Dumas et al., 2015). The two strains can be differentiated using molecular markers, specifically polymorphism in the mitochondrial cytochrome oxidase 1 (CO1) gene (Ke & Pashley, 1992; Nagoshi et al., 2012).

Spodoptera frugiperda originates from tropical and subtropical regions of the United States (Luginbill, 1928; Rwomushana, 2019; Sparks, 1979). *Spodoptera frugiperda* has spread to almost every part of the world except Europe and Antarctica (EPPO, 2024;

Rwomushana, 2019). It was first recorded in Central and West Africa in early 2016 (Goergen et al., 2016). By 2017, *S. frugiperda* had spread to all sub-Saharan African countries except Lesotho (Food and Agriculture Organization of the United Nations [FAO], 2017). In 2018, it was first found in the districts of Shivamogga and Navanagere in Karnataka, India (Ganiger et al., 2018; Sharanabasappa et al., 2018; Shylesha et al., 2018). The following year, *S. frugiperda* was recorded in Bangladesh, Myanmar, Sri Lanka, Thailand, Vietnam, Indonesia, China, and Malaysia (Lamsal et al., 2020). Morphological and molecular identification confirmed that pest samples from maize fields in Chuping, Perlis (near the Malaysia-Thailand border) were *S. frugiperda* (IPPC, 2019). By early 2020, *S. frugiperda* had been detected in all states of Malaysia (Jamil et al., 2021b).

BIOLOGY OF FALL ARMYWORM (FAW), SPODOPTERA FRUGIPERDA

The ability of *S. frugiperda* to migrate and cause repeated attacks in both native and new areas is facilitated by various biological traits such as strong flight capability, polyphagous feeding habits, high fecundity, and significant ecological resilience (FAO & PPD, 2020; Montezano et al., 2018). *Spodoptera frugiperda* has no diapause mechanism and cannot survive in winter in northern parts of America, prompting migration to the warmer southern regions (Rose et al., 1975). Low temperatures reduce flight speed and wingbeat frequency, and the flight performance of *S. frugiperda* moths is abysmal at 10°C (Ge et al., 2021). Nocturnal in nature, *S. frugiperda* moths can fly up to 100 km overnight (Assefa & Ayalew, 2019; Johnson, 1987; Sparks, 1979). Ge et al. (2021) found that 84% of *S. frugiperda* moths flew more than 40 km, covering a total distance of 163.58 km over five days. *Spodoptera frugiperda* undergoes complete metamorphosis, transitioning through egg, larval, pupal, and adult stages. The development of S. *frugiperda* depends on the larval food source, as in Table 1 and Table 2.

Tables 1 and 2 comprehensively compare various parameters related to the biology and development of *S. frugiperda* (fall armyworm) across different host plants and conditions. These parameters include fecundity, egg incubation, larval and pupal periods, adult emergence, and longevity. The data is derived from multiple studies conducted in different countries. The highest fecundity is observed on an artificial corn-based diet (1746.3 eggs/female), while the lowest is recorded on sorghum (106.44 eggs/female). However, the absence of data on several parameters for this diet (pupation percentage, adult emergence) leaves gaps in fully understanding its effects. Among natural plants, maize variants (fodder maize, field maize, sweet maize) generally support higher fecundity and faster development compared to other crops like sorghum and rice, which suggests that maize could be a more suitable host for *S. frugiperda*. The larval period ranges from 10.83 days on sweet maize to 21.28 days on sunn hemp, indicating that the host plant choice significantly affects the time required for larval development. Pupal periods also vary, with some values not provided

(No data, ND) for several plants. However, available data shows the shortest pupal period on rice leaves (7.03 days for males) and the longest on corn var. NK 6410 (7.98 days for males). The total life cycle period spans from 24.58 days on corn var. Macho F1 to 48.61 days on rice leaves, reflecting the host plant's impact on the overall development speed of *S. frugiperda*. The data in Tables 1 and 2 underscores the significant effect of host plants on the biological traits of *S. frugiperda*. This variability is crucial for understanding the pest's adaptability and developing targeted management strategies.

DAMAGE AND LOSSES DUE TO FAW LARVAE INFESTATION IN MAIZE FIELD

Larvae of *S. frugiperda*, particularly from the third to the sixth instar, have caused more than 70% damage to corn crops (Assefa & Ayalew, 2019). *Spodoptera frugiperda* attacks reported in maize fields in Nicaragua, Central America, have resulted in yield losses ranging from 15% to 73%, with an attack rate of 55% to 100% (Hruska & Gould, 1997). Fall armyworm (FAW) larvae attacks in Ghana, Zambia, and Cameroon have caused crop yield losses ranging from 0.3 to 20.5 million tons, valued at US$0.1 to 6.2 billion (Day et al., 2017). In Malaysia, *S. frugiperda* infestations have caused severe attacks (100%) in maize fields in Changlun, Kedah, severely damaging all parts of the corn plants (Jamil, Saranum, Saleh-Hudin et al., 2021). Maize fields affected by *S. frugiperda* attacks covered an area of 246.35 hectares, with an infestation severity percentage ranging from 50% to 100% (IPPC, 2019).

CONTROL AND MANAGEMENT OF FALL ARMYWORM (FAW), SPODOPTERA FRUGIPERDA

Regular monitoring and early detection are vital in managing and controlling infestations of *S. frugiperda* to prevent economic damage to crops (Assefa & Ayalew, 2019). For infestations with less than 5% of seedlings or 20% of corn plants under 30 days old, curative control using chemical insecticides is recommended (EPPO, 2024). The economic threshold level (ETL) for this pest in hybrid maize and sorghum crops is 1.8-2.5 larvae/10 plants and 1-2 larvae/plant, respectively (Jaramillo-Barrios et al., 2020; Pitre, 1985). Meanwhile, the economic injury level (EIL) on maize is 14%, 21%, 23%, 26%, and 50% infestation by *S. frugiperda* at 2, 3, 4, 5, and 6 weeks after crop germination (Evans & Stansly, 1990).

Chemical insecticides are the primary method to control *S. frugiperda* larvae in the Americas and Africa (Otim et al., 2021). Commonly used active ingredients include Emamectin benzoate, Chlorantraniliprole, Spinetoram, Diamides, Avermectin, Spinosad, and Indoxacarb (Bird et al., 2022; Otim et al., 2021; Sarkowi & Mokhtar, 2021). Reliance on chemical control strategies on a global scale for several decades has led to resistance in *S. frugiperda* to at least 29 active ingredients across six mode-of-action groups (Bird et al.,

Table 1
Development performance of Spodoptera frugiperda *based on host plant*

Plant/ Parameter	Egg Incubation period (days)	Larval period (days)	Pupal period (days)	Oviposition period (days)	Adult longevity (days)		Total life cycle period (days)		Country	Reference
					M	F	M	F		
Pearl millet	2 ± 0.43	16.93 ± 0.61	7.61 ± 0.38	1.20 ± 0.03	4.31 ± 0.05	6.80 ± 0.06	30.85 ± 0.46	33.34 ± 0.52	India	Bankar and Bhamare (2023a)
Sugar cane	2.52 ± 0.30	19.17 ± 0.51	8.49 ± 0.42	1.36 ± 0.04	4.18 ± 0.09	5.86 ± 0.04	34.36 ± 0.80	36.04 ± 0.51		
Fodder maize	2.17 ± 0.00	ND	9.05 ± 0.21	4.25 ± 0.75	7.00 ± 0.05	7.00 ± 0.41	ND	ND	Egypt	Mohamed et al. (2023)
Corncobs	2.51 ± 0.00	NE	7.76 ± 0.28	5.00 ± 0.55	8.50 ± 0.29	10.00 ± 0.41	NE	NE		
Maize leaves	2.66 ± 0.57	16.65 ± 0.61	ND	ND	16.13 ± 1.02	16.89 ± 0.55	43.79 ± 0.99	44.55 ± 0.59	Indonesia	Maharani et al. (2021)
Rice leaves	3.00 ± 0.00	20.32 ± 0.68	ND	ND	16.71 ± 0.93	18.94 ± 1.50	43.79 ± 0.99	48.61 ± 0.55		
Sorghum	2.26 ± 0.21	15.93 ± 0.94	7.99 ± 0.24	1.14 ± 0.05	5.13 ± 0.07	6.34 ± 0.03	31.31 ± 0.77	32.52 ± 0.44	India	Bankar & Bhamare (2023b)
Maize	2 ± 0.33	12.58 ± 0.75	6.74 ± 0.44	1.88 ± 0.04	6.29 ± 0.09	8.46 ± 0.03	27.61 ± 0.60	29.78 ± 0.66		
Maize leaves	3-4	16.6 ± 0.82	9.2 ± 1.64	2.8 ± 0.27	10.4 ± 0.41	12.4 ± 0.54	36.2 ± 1.25	38.2 ± 1.35	India	Aarthi-Helen et al. (2021)
Traditional corn (Tinigib)	ND	14.07 ± 0.44	8.09 ± 0.26	3.80 ± 0.38a	8.93 ± 1.14	10.13 ± 1.02	25.31 ± 0.57		Philippines	Agravante et al. (2023)
Corn var. Macho F1	ND	13.52 ± 0.36	8.02 ± 0.33	3.78 ± 0.25	9.07 ± 0.43	9.98 ± 0.49	24.58 ± 0.44			
Corn var. NK 6410	ND	13.60 ± 0.44	7.98 ± 0.29	4.00 ± 0.33	9.20 ± 0.38	10.40 ± 0.86	24.66 ± 0.33			
Rice var. RC 226	ND	14.41 ± 0.19	8.81 ± 0.57	2.80 ± 0.69	8.80 ± 0.77	9.80 ± 0.70	26.45 ± 0.62			
OPV Corn	ND	14.49 ± 0.39	8.65 ± 0.35	3.33 ± 0.24	9.13 ± 0.69	10.40 ± 0.60	26.36 ± 0.47			
Napier grass	2.00 ± 0.00	16.74 (F) 21.16 (M)	7.26 ± 0.08 8.71 ± 0.09	8.20 ± 0.46	12.55 ± 0.82	14.40 ± 0.88	26.90 ± 0.21	25.13 ± 0.21	Taiwan	Chen et al. (2023)
Natal grass	2.00 ± 0.00	21.18 (F) 20.95 (M)	7.03 ± 0.06 8.02 ± 0.06	6.17 ± 0.40	8.67 ± 0.42	9.41 ± 0.39	27.26 ± 0.16	26.11 ± 0.17		
Sunn hemp	2.00 ± 0.00	19.85 (F) 21.28 (M)	6.96 ± 0.07 7.93 ± 0.06	6.78 ± 0.57	10.31 ± 0.57	11.78 ± 0.56	25.41 ± 0.24	24.00 ± 0.18		
Field maize	2.00 ± 0.00	11.28 ± 0.05	7.93 ± 0.09	3.33 ± 0.33	4.82 ± 0.46	5.64 ± 0.44	28.26 ± 0.39	27.96 ± 0.41	Thailand	Hong et al. (2022)
Sweet maize	2.03 ± 0.02	10.83 ± 0.14	7.57 ± 0.09	3.00 ± 0.58	4.71 ± 0.42	6.13 ± 0.35	26.90 ± 0.37	27.42 ± 0.36		

Table 1 *(continue)*

Plant/ Parameter	Egg Incubation period (days)	Larval period (days)	Pupal period (days)	Oviposition period (days)	Adult longevity (days)		Total life cycle period (days)		Country	Reference
					M	F	M	F		
Waxy maize	2.02 ± 0.01	11.15 ± 0.15	8.24 ± 0.09	4.00 ± 0.00	4.53 ± 0.52	5.35 ± 0.43	28.61 ± 0.30	28.21 ± 0.38		
Artificial corn-based diet	ND	15.3 ± 0.15	11.3 ± 0.20	ND	ND	ND	ND	ND	Brazil	Pinto et al. (2019)

Note. M = Male, F = Female, ND = No Data

Table 2
Reproductive performance of Spodoptera frugiperda *based on host plant*

Plant/Parameter	Larval weight (g)	Pupal weight (g)	Pupation (%)	Adult emergence (%)	M: F ratio	Country	Reference
Pearl millet	ND	ND	71 ± 1.06	86 ± 0.50	1:1.26	India	Bankar and Bhamare
Sugar cane	ND	ND	85 ± 0.74	87 ± 0.37	1:1.19		(2023a)
Fodder maize	0.34 ± 0.008	0.16 ± 0.004	ND	ND	3: 5	Egypt	Mohamed et al. (2023)
Corncobs	0.41 ± 0.01	0.20 ± 0.005	ND	ND	8:13		
Maize leaves	ND	ND	ND	ND	1.03:1	Indonesia	Maharani et al. (2021)
Rice leaves	ND	ND	ND	ND	1.04:1		
Sorghum	ND	ND	91±1.17	91±0.69	1:1.31	India	Bankar and Bhamare
Maize	ND	ND	88±0.84	92±0.49	1:1.20		(2023b)
Traditional corn (Tinigib)	ND	ND	ND	94.00 ± 8.40	50:50	Philippines	Agravante et al. (2023)
Corn var. Macho F1	ND	ND	ND	100 ± 0.00	60:40		
Corn var. NK 6410	ND	ND	ND	100 ± 0.00	36:64		
Rice var. RC 226	ND	ND	ND	88.00 ± 10.95	48:52		
OPV Corn	ND	ND	ND	94.67 ± 8.69	51:49		
Field maize	ND	ND	89.06	ND	7.25: 6.5	Thailand	Hong et al. (2022)
Sweet maize	ND	ND	85.71	ND	7.25: 7.75		
Waxy maize	ND	ND	92.31	ND	8: 9.75		
Artificial corn-based diet	ND	0.259 ± 0.003	89.3 ± 7.59	ND	0.55 ± 0.07	Brazil	Pinto et al. (2019)

Note. M = Male, F = Female, ND = No Data

2022). Within Integrated Pest Management (IPM), chemical insecticides are considered a last resort to curb crop pest infestations (Day et al., 2017).

Biological control, mainly using microbes such as bacteria, fungi, viruses, and entomopathogenic nematodes, has also been employed to manage *S. frugiperda* infestations (Guo et al., 2020). *Bacillus thuringiensis* causes 61%–87% larval mortality in the field and 100% in the laboratory (Liu et al., 2019). Spraying *nucleopolyhedrovirus (NPV)* in maize fields has resulted in 93.4% larval mortality of *S. frugiperda* (Cruz et al., 1997). Using a combination of viruses, such as *S. frugiperda multiple nucleopolyhedroviruses (SfMNPV)* and *S. frugiperda granulovirus (SfGV),* can enhance virus efficacy and help delay resistance evolution (Hussain et al., 2021). The use of entomopathogenic fungi such as *Beauveria bassiana* and *Metarhizium anisopliae* has been reported to cause 64.3% and 67.8% larval mortality of *S. frugiperda* in the laboratory (Ramanujam et al., 2020).

ENTOMOPATHOGENIC NEMATODES (EPN) AND THEIR SYMBIOTIC BACTERIA

Entomopathogenic nematodes (EPNs) are a group of nematodes that infect and kill insects. Entomopathogenic nematodes (EPNs) reside in the soil and are obligate parasites from the Phylum Nematoda (Gozel & Gozel, 2016). The first EPN, identified as *Aplectana kraussei* (now known as *Steinernema kraussei*), was described by Steiner in 1923 (Poinar & Grewal, 2012). Steinernematidae comprises two genera, *Steinernema* (with more than 50 species) and *Neosteinernema* (one species: *Neosteinernema longicurvicauda*). The family Heterorhabditidae is monotypic, containing only one genus, *Heterorhabditis*, with one species, *Heterorhabditis bacteriophora* (Gozel & Gozel, 2016; Stock & Blair, 2008). Poinar (1976) described the first Heterorhabditis in 1976. Hunt and Nguyen (2016) reported that by the end of 2015, 95 species of *Steinernema* and 16 species of *Heterorhabditis* had been identified. Entomopathogenic nematode (EPN) species identification is based on morphological and morphometric data comparisons and cross-breeding tests (Gaugler, 2002). Diagnostic methods like Polymerase Chain Reaction (PCR), PCR-RFLP, and Random Amplified Polymorphic DNA (RAPD) are employed to identify EPN species based on dioxyribonucleic acid (DNA) sequence comparisons (Caoili et al., 2018; Stock & Blair, 2008). Two families are widely used as effective biological control agents for managing pests above and below the soil: Steinernematidae and Heterorhabditidae (Kaya et al., 2006; Vashisth et al., 2015).

Entomopathogenic nematodes (EPNs) are capable of infecting and thriving within a wide range of insects, completing their life cycle in species from orders such as Lepidoptera, Coleoptera, Orthoptera, Diptera, Thysanoptera, and Siphonaptera (Půža & Mráček 2010). The life cycle of EPNs begins with the third stage, infective juvenile (IJ), which is free-living in the soil, capable of infecting the target host, and the only stage found outside the

host. Entomopathogenic nematodes (EPNs) in the soil detect target hosts by responding to carbon dioxide, vibrations, chemical signals/stimuli, or sensing the physical structure of the insect's integument (Gaugler, 2002). The life cycle of EPN is shown in Figure 1. Entomopathogenic nematodes (EPNs) are associated with symbiotic bacteria from the family Enterobacteriaceae. Steinernematidae is associated with symbiotic bacteria from the genus *Xenorhabdus*, while Heterorhabditidae is associated with symbiotic bacteria from the genus *Photorhabdus* (Gozel & Gozel, 2016; Vashisth et al., 2013). Symbiotic bacteria, *Xenorhabdus* and *Photorhabdus*, kill the insect host quickly, create a suitable environment for EPN reproduction, produce antibiotics and secondary metabolites that inhibit the growth of other microorganisms, and convert host tissue into food (Forst & Nealson, 1996). In exchange, EPNs provide protection and access to the host insect's hemolymph (Vashisth et al., 2013).

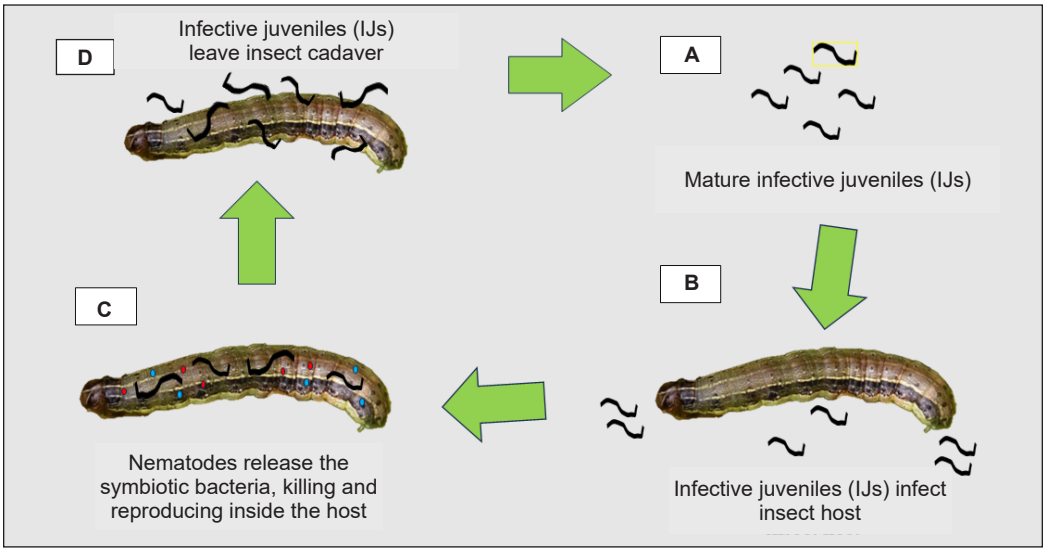

Figure 1. Illustration of the life cycle of entomopathogenic nematodes on insect host. (A) Mature infective juveniles (IJ3) find a host in the soil. (B) Infective juveniles (IJs) enter the host via the mouth, anus, and spiracle opening. (C-D) Infective juveniles (IJs) infect and release symbiotic bacteria to elude the host immune system and kill the host. Both species (nematode and symbiotic bacteria) reproduce using the cadaver's nutrients; when the nutrients are impoverished, the two creatures recombine and enter the soil to restart the cycle

BIOLOGICAL CONTROL OF FALL ARMYWORM (FAW), SPODOPTERA FRUGIPERDA USING ENTOMOPATHOGENIC NEMATODES (EPN)

Researchers from different countries have conducted various studies on the pathogenicity of entomopathogenic nematodes against *S. frugiperda* (Guo et al., 2020). Rodríguez-Zamora (2019) reported that the entomopathogenic nematode (EPN), *Heterorhabditis bacteriophora*, caused 65% mortality in *S. frugiperda* larvae in the laboratory within 48

hours. *Heterorhabditis bacteriophora* also caused 92% and 80% mortality in pre-pupae and pupae of *S. frugiperda*, respectively (Alonso & Mejia, 2018). Meka et al. (2020) stated that the highest larval mortality of *S. frugiperda*, 100%, occurred when infected with *Steinernema glaseri* at a concentration of 2000 IJs/plate, followed by 95% at 1000 IJs/plate after 96 hours of inoculation. Due to the high pathogenicity of insect hosts, various EPN species have been studied for their potential as biological control agents against *S. frugiperda* (Table 3).

The studies presented in Table 3 are a comprehensive summary of various studies investigating the effectiveness of different entomopathogenic nematode (EPN) species against the fall armyworm (FAW), *Spodoptera frugiperda*, under various conditions, including laboratories, fields, greenhouses, and across different countries. A variety of EPN species, such as *Steinernema sp.*, *Heterorhabditis indica*, *S. carpocapsae*, and others, were tested against different developmental stages of FAW larvae (third instar, sixth instar, pre-pupae, and pupae). The concentrations of EPNs used in these studies varied significantly, ranging from as low as five infective juveniles (IJs) per larva to as high as 50,000 IJs per plant in field trials. The duration of exposure also differed across studies, from as short as 14 hours to as long as 25 days. The results indicate that the effectiveness of EPNs in causing mortality in FAW larvae is highly dependent on the EPN species, concentration, and environmental conditions. For instance, *Steinernema sp*. and *Heterorhabditis sp*. showed a mortality rate of 100% in certain laboratory conditions. Studies with combinations of EPNs and other biocontrol agents, like *Metarhizium anisopliae* or insecticides, demonstrated varying levels of success, highlighting the potential for integrated pest management approaches.

Species of entomopathogenic nematodes (EPNs) outperform others under certain conditions due to biological, ecological, and environmental factors. Based on the provided data (Table 3), the key reasons are symbiotic bacteria efficacy, host stage suitability, application techniques, synergistic combinations, and speed of host mortality. Entomopathogenic nematodes (EPNs) are closely associated with specific symbiotic bacteria, such as *Photorhabdus* in *Heterorhabditis* and *Xenorhabdus* in *Steinernema*. The virulence of these bacteria varies, affecting the speed and efficiency of killing the host insect (Owuama, 2001). Different EPN species more effectively target specific developmental stages of the FAW. For instance, *Steinernema carpocapsae* showed 100% mortality in second and third-instar larvae, whereas higher doses of *Heterorhabditis bacteriophora* were required for similar effects on pre-pupae and pupae. The concentration of infective juveniles (IJs) and delivery methods significantly impact outcomes. Higher concentrations, such as 2000 IJs per plate for *Steinernema glaseri*, result in more excellent mortality rates than lower doses. Moreover, species like *S. carpocapsae* are known for rapid action due to their ambush strategy, while others, like *H. bacteriophora*, adopt a more cruising approach, affecting their performance under specific conditions (Stock & Blair, 2008).

Overall, the studies summarized in Table 3 illustrate the potential of EPNs as biocontrol agents against FAW, with varying degrees of success influenced by multiple factors. The data suggest that laboratory conditions often yield higher mortality rates, while field applications may require combination treatments and further optimization to achieve consistent results. The table also underscores the global research interest in EPNs, with studies conducted across different continents emphasizing the universal challenge posed by FAW and the widespread efforts to manage this pest.

ENTOMOPATHOGENIC NEMATODES (EPN) AS BIOPESTICIDES AND THEIR APPLICATION IN INTEGRATED PEST MANAGEMENT (IPM)

Countries that have commercialized EPN as biopesticides include Sanoplant (Switzerland), Helix (Canada), ORTHO Biosafe USA (United States), Koppert (Netherlands), and BASF (Germany). Entomopathogenic nematode (EPN) can be stored and produced in large quantities *in vivo* and *in vitro* (Shapiro-Ilan et al., 2012). At least 13 species of Steinernematidae and Heterorhabditidae have been commercialized for pest control (Shapiro-Ilan et al., 2016). In the laboratory, EPN can be inoculated onto insect hosts using Petri dishes and filter papers with a minimum concentration of EPN before being transferred to White Traps for *in vivo* collection (Shapiro-Ilan et al., 2012). However, mass production of EPN can be carried out *in vitro* using solid or liquid culture media (McMullen & Stock, 2014). The *in vitro* liquid method is the most cost-effective way to produce nematodes, followed by the *in vitro* solid method. In contrast, the *in vivo* method is the least economical. While *in vitro* techniques allow for large-scale, affordable production ideal for treating vast field areas to control crop pests, the *in vivo* method is more costly. It produces nematodes in smaller quantities, making it better suited for nursery soil treatments or small plots (Askary & Ahmad, 2017).

Mass production of EPN allows for the creation of biopesticide products. EPN formulation occurs when the active ingredient (EPN) combines several materials, such as sunscreens, additives, and carriers. Entomopathogenic nematode (EPN) biopesticides can be produced as aqueous solutions, synthetic sponges, gels, and clay powders to facilitate storage and transportation (Cruz-Martínez et al., 2017). Since EPNs are sensitive to ultraviolet (UV) radiation, EPN sprays should be done in the late afternoon (Negrisoli et al., 2010).

Entomopathogenic nematodes (EPNs) are critical components of integrated pest management (IPM) systems and have practical applications in managing fall armyworms (FAW) and other agricultural pests. These essential applications include EPNs being an eco-friendly replacement for chemical insecticides; they fit the IPM principle of minimizing chemical inputs while maintaining effective pest control (Day, 2017). Combining EPNs with biopesticides such as *Metarhizium anisopliae* or *Bacillus thuringiensis* (Bt) could increase

Table 3
Studies on the pathogenicity of entomopathogenic nematodes against the fall armyworm, Spodoptera frugiperda

EPN species	Condition	FAW stage	Concentration	Duration	Result (% Mortality)	Symbiotic bacteria	Country	Reference
Steinernema sp. *Heterorhabditis indica*	Laboratory	100 third instar larvae	0, 50, 100, 200 and 400 IJ/ml per larvae	14 h	• 100% (200IJ) • 75% (400IJ)	ND	Brazil	Garcia et al. (2008)
H. indica, *S. carpocapsae* *S. glaseri*	Laboratory	11 200 third instar larvae	100IJ/container + Half dose insecticides	4 d	• 88%–90% • 94%–98% • 98%–100%.	ND	Brazil	Negrisoli et al. (2010)
H. indica	Field	Maize	250IJ/ cm2 + Luferon/ Chlorpyrifos	2 y	• 62.5% (Year 1) and 57.5% (Year 2)—Combination of *H. indica* and lufenuron (0.15 L/ha)			
S. arenarium *Heterorhabditis sp.* RSC02	Laboratory	80 fourth or fifth instar larvae	0, 100, 250, and 500 IJ/ml per larvae	72 h	• 80% and 100% • 85% and 97.6%	ND	Brazil	Andaló et al. (2010)
S. arenarium *Heterorhabditis* sp. RSC02	Glasshouse	40 fourth or fifth instar larvae	200IJ/container	96 h	• 75% • 87.5%			
Heterorhabditis sp. (2) *Steinernema* sp.	Laboratory	200-fifth instar larva	100 and 300µl IJ per larva	120 h	• 70%–80% • 28%–56%	• *Photorhabdus luminescens* subsp. *Laumondii* • *Xenorhabdus szen- tirmaii*	Brazil	Salvadori et al. (2012)
H. amazonensis RSC2 *S. arenarium* A11	Laboratory	20 larvae	500 IJ/10 ml per larva	6 d	• 100% • 100%	ND	Brazil	Andaló et al. (2012)
S. diaprepesi	Laboratory	45 sixth instar larvae	0, 50, and 100 IJ/0.5 ml per larva	6 d	93% (50 IJ) and 100% (100 IJ)	ND	Argentina	Caccia et al. (2014)

Table 3 *(continue)*

EPN species	Condition	FAW stage	Concentration	Duration	Result (% Mortality)	Symbiotic bacteria	Country	Reference
H.bacteriophora	Field	1 larva per corn cob	250 EPN/plant	5d	• 100% (*H. bacteriophora* + *Metarhizium anisopliae*) • 93.33% (*H. bacteriophora* + *M. anisopliae* + Chlorpyrifos)	ND	Costa Rica	Bissiwu & Pérez (2016)
H. indica	Laboratory	60 sixth instar larvae	200 IJ/ml per larva and 1–104 CFU/ larva (symbiotic bacteria	72h	Symbiotic bacterial extracts (intra- and extracellular) caused 10% and 93% larval mortality	*Photorhabdus luminescens subsp. akhurstii* SL0708	Colombia	Salazar-Gutiérrez et al. (2017)
S. carpocapsae	Laboratory	60 larvae	200µl/larva	96h	90% within 72h (*S. carpocapsae* + chlorantraniliprole or spinetoram at high doses	ND	Puerto Rico, USA	Viteri et al. (2018)
H. bacteriophora	Laboratory	240 pre-pupae and pupae	1000, 3000 and 5000 EPN/ml	72h	• 75%, 87% and 92% (pre-pupae) • 55%, 70% and 80% (Pupae)	ND	Peru	Alonso & Mejia (2018)
	Glasshouse	80 pre-pupa and pupa		120h	• 68%, 70% and 78% (pre-pupae) • 48%, 53% and 62% (pupae)			
S. carpocapsae (strain SK27)	Laboratory	24 sixth instar larvae	150 IJ/150µl per larva	48h	100%	*Xenorhabdus nematophila*	France	Huot et al. (2019)

Table 3 *(continue)*

EPN species	Condition	FAW stage	Concentration	Duration	Result (% Mortality)	Symbiotic bacteria	Country	Reference
H. bacteriophora *H. indica*	Laboratory	125 second instar larvae	0, 20, 40, 80 and 170 IJ/larva	5d	• 65% in 48h (40IJ), LC_{50}= 32 IJ/ml • 65% in 48 (170IJ), LC_{50}= 42 IJ/ml	*Photorhabdus luminescens*	Nicaragua	Rodríguez-Zamora (2019)
H. indica *H. bacteriophora,* *Heterorhabditis sp.* *S. carpocapsae* *S. arenarium* *S. longicaudum*	Laboratory	All larva stages pupae	250 IJ/ml, 600 IJ/5ml and 25 IJ/ cm^2	5d	100% (*H. indica* and *S. carpocapsae)* against first and second instar larvae	ND	South Korea	Acharya et al. (2020)
S. glaseri	Laboratory	All larva stages	0, 250, 500, 1000 and 2000 IJ/Petri dish	96j	• 100% (2000IJ) • 95% (1000IJ)	ND	India	Meka et al. (2020)
Steinermatidae sp. (Kepahiang) *Steinermatidae sp.* (Bengkulu)	Laboratory	15 third instar larvae	0 IJ/ml, 200 IJ/ml, 400 IJ/ 2ml, 600 IJ/3ml per larva	5d	• 60%, 80% and 100% (LC_{50}=163.5 IJ/ml) • 46.6%, 73.3% and 93.3% (LC_{50}= 186.5 IJ/ml)	ND	Indonesia	Hade et al. (2020)
H. ruandica *Steinernema sp.* *S. carpocapsae*	Laboratory	24 second, third, and six instar larvae for each treatment	5, 10, 25, 125 IJ/400µl per larva	7d	*S. carpocapsae* from Rwanda caused 100% rapid mortality in second and third-instar larvae and 75% in sixth-instar larvae.	ND	Rwanda	Fallet et al. (2022)
H. indica	Laboratory	Third, fourth, and fifth instar larvae	10, 20, 40, 60, 80, 100, 120, 140, and 160 IJs/larva	96h	100% (160IJs/larva)	ND	India	Shinde et al. (2023)

Table 3 *(continue)*

EPN species	Condition	FAW stage	Concentration	Duration	Result (% Mortality)	Symbiotic bacteria	Country	Reference
S. carpocapsae	Field	Maize	200, 400, and 500 IJs per treatment	25d and 40d	*S. carpocapsae* @ 500 IJs significantly reduced the larval population and leaf damage score	ND	India	Ratnakala et al. (2023)
H. bacteriophora	Laboratory	Third and fifth instar larvae	60, 120, 250, 500, 1000, 2000 and 5000 IJs/ml	48h	78.33% to 100%	ND	China	Chen et al. (2023)
	Glasshouse	Third instar larvae	5000, 10,000 and 20,000 IJs/500ml	72h	51.56% at 48h and 68.72% at 72h (2000 IJs)			
	Field	Maize	10,000/25,000/ 50,000 IJs per plant	14d	43.18% (10,000/plant), 51.20% (25,000/plant), 25.17% (50,000/plant) after 48h			
S. carpocapsae *H. indica*	Laboratory	Second to sixth instar larvae	150, 300, 600, 1200 and 2400 IJs/ larvae/ml	188h	• 100% after 48-72h • 100% after 96h	ND	Egypt	Mohamed and Shairra (2023)
H. indica *S. abbasi*	Laboratory	Fifth instar larva	200IJ/150µl/plates	48h	• 100% • 100%	ND	Philippines	Duza et al. (2024)
S. carpocapsae	Field	Maize	1,500 EPN/ml / 3,000 EPN per plan	7d and 14d	Decreased larvae infestation by about 50%	ND	Rwanda	Fallet et al. (2024)
H. alii.	Laboratory	Third, fourth, fifth and sixth larval instars	100, 250, and 500 IJs/ml	72h	100% for all tested instar larvae	ND	Egypt	Shamseldean et al. (2024)
S. aciari	Laboratory	Third and sixth instar larvae	40, 60, 80, 100 IJ/ larva	96h	52%, 68%, 88% and 92% (third instar larvae)	ND	China	Sun et al. (2024)

Note. ND = No data

mortality rates and broaden the pest control spectrum (Bissiwu, 2016). Entomopathogenic nematodes (EPNs) can also be applied alongside cultural control practices like pheromone traps or crop rotation, creating a multi-layered pest management strategy. EPNs are effective against various FAW life stages, including larvae, pre-pupae, and pupae (Table 3). This capability makes them versatile IPM components capable of reducing pest populations at multiple points in their lifecycle. Unlike chemical insecticides, EPNs do not induce resistance in pests. This characteristic makes them valuable in IPM, which aims to sustain long-term pest suppression without escalating resistance risks. Entomopathogenic nematodes (EPNs) can be applied using standard agricultural equipment, either as soil treatments or foliar sprays, making them easy to integrate into existing farming practices (Shapiro-Ilan et al., 2012).

CONCLUSION

Based on the review of various articles, thesis, and books regarding the pathogenicity of EPNs and their symbiotic bacteria against the fall armyworm (FAW), *S. frugiperda*, there is potential for EPN (either local isolates or imported) to be developed as effective biological control agents in Malaysia. This manuscript highlights significant gaps and underexplored aspects in applying EPNs as biocontrol agents for managing FAW *Spodoptera frugiperda* in Malaysia and beyond. The key contributions are field-level efficacy, environmental constraints, local adaptation, and EPN formulations. The need for extensive field-based studies on EPN pathogenicity against FAW is identified. Environmental factors like UV radiation, soil composition, and moisture levels can significantly affect EPN efficacy. Developing formulations or application strategies to overcome these challenges is crucial. Moreover, research on identifying and testing local EPNs is essential as local EPN isolates in Malaysia suggest that locally adapted species may perform better in Malaysia's environment.

Using EPNs as biological control agents in Malaysia will significantly affect the country's agricultural landscape and policy frameworks. Potential impacts and considerations include reducing chemical dependency, increasing food sustainability, and improving yield protection. Although biopesticides' initial costs may be higher than traditional pesticides, long-term savings through reduced pest resistance and ecosystem restoration can make EPNs economically viable. Nevertheless, promoting EPN-based products could spur local industries into biopesticide manufacturing, reducing reliance on imports and creating jobs. Besides, research into native species can optimize efficacy and reduce dependency on imported strains. Expanding field-level research will demonstrate EPN's effectiveness to farmers, increasing adoption rates. Policies promoting the adoption of EPNs, such as subsidies for biopesticides or incentives for sustainable practices, could accelerate their integration into pest management strategies. Training and awareness

programs that educate farmers about EPNs, including their benefits and application methods, are critical to overcoming resistance to adopting new practices. Adopting EPNs in Malaysia could revolutionize pest management practices, enhance sustainability, and reduce reliance on chemical solutions. These benefits align with national priorities, including environmental conservation, agricultural productivity, and food security, while fostering innovation and policy evolution in the agricultural sector.

Therefore, future research should prioritize formulating EPNs, IPM approaches, combining biocontrol measures with sustainable agricultural practices to enhance efficiency and minimize environmental impact. Government agencies and local and international organizations also play a role in providing knowledge and advisory services. Policies such as providing biopesticide subsidies to farmers should be established to encourage the use of biopesticides.

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