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RESEARCH

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Pathogenicity of entomopathogenic nematodes against the new invasive fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae)

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Abstract

Background Fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is the new invasive pest of different economic crops, threatening the agricultural economy worldwide. Chemical insecticides are the main control management strategy applied by almost farmers. As the adverse effect of these chemicals on the environment and human health, improving alternative environmentally friendly control against this pest is urgently needed. In this response, the pathogenicity bioassays of 2 entomopathogenic nematode species (EPNs), *Steinernema carpocapsae* (All) and *Heterorhabditis indica* (EGAZ2), on different FAW larval instars (2nd to 6th instars) were assessed under laboratory conditions.

Results The results cleared that FAW larval mortality rate was varied significantly related to nematode species, post-exposure times and developmental instar stages. *S. carpocapsae* application was more virulent and effective against all tested instars larvae, registering 100% mortality after 48–72 h post-exposure at different nematode concentrations (150–2400 IJs). However, *H. indica* caused 100% mortality in early instars only after 96 h, but late instars required a longer time extending to 120–188 h at tested concentrations. In this context, 2nd and 3rd instars were highly susceptible to *Heterorhabditis* species infection. Lower nematode concentrations (150–300 IJs) caused moderate mortality 33.33–50%, respectively, in 5th and 6th full-developed larvae only. All recovery larvae post-infection died in the pupal stage or adult emerged with wing malformation.

Conclusion The 2 EPN species were virulent against different FAW larval instars at different concentrations and exposure times. Thereby, they are recommended as biocontrol agents against this invasive pest, particularly *S. carpocapsae* after low-exposure time. This study provides essential information on EPNs, which will further help in the practical application of biological control against fall armyworm.

Keywords Biological control, Entomopathogenic nematodes, *Spodoptera frugiperda*, Pathogenicity assays

Background

One of the most threats to food security and income of many millions' smallholder farmers and consumers in recent years is the invasion of fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) (FAO 2019). This quarantine pest attacked more economical crops such as maize, sorghum, rice, cotton, wheat, sugarcane, peanut, soybean, cabbage, beet, alfalfa, onion,

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millet, tomato and potato (CABI 2020), with maize being the most preferable host (FAO 2017). The main problem of this destructive pest was related to the high dispersal ability, more fecundity rate (> 2000 eggs), long-distance migratory behavior over 500 km, continuous generations per year and adaptability to climate conditions and strong flier up to 100 km per night (Mohamed 2022). This pest was first observed on maize fields in 2019 at Aswan Governorate, Upper Egypt (Dahi et al. 2020). Within a short period of its invading, it has further infested almost all Egypt Governorates by the late of 2021 (Mohamed et al. 2022). Different control methods have been applied in an attempt to get rid of this pest, but farmers still depend on conventional and new chemical insecticides. Excessive and continuous uses of the major classes of these chemicals have developed high resistance against them (Wan et al. 2021). Furthermore, chemical control has not provided a long-term solution for pest problems due to the adverse effect on natural enemies, pollinators and biodiversity, environmental pollution, minor pests' resurgence and human health, especially the applicator (Akhtar and Farooq 2019). In addition, *Bacillus thuringiensis* (Bt) was used previously as a biocontrol agent against FAW, but it also has developed its resistance to *Bt* toxins (Murŭa et al. 2019). Therefore, there is a mounting need to develop alternate, non-chemical tools and effective environmentally friendly methods to suppress the FAW infestation. Among the eco-friendly management strategies, biological control by natural enemies (parasitoids, predators and pathogens) is highly recommended. In this concept, entomopathogenic nematodes (EPNs) belonging to Steinernematidae and Heterorhabditidae (Rhabditida) families have been widely used as promising biocontrol agents in the last few decades on various economic insect pests (Thakur et al. 2022). Additionally, these EPNs are associated with symbiotic pathogenic bacteria (*Xenorhabdus* and *Photorhabdus*) (Stock 2019), penetrating the insect host through natural opening such as cuticle, mouth, anus or spiracles to reach the hemocoel and release their bacteria to multiply rapidly into hemolymph, degrading the insect tissue and producing many immune-suppression factors against the target host as antimicrobial compounds, hydrolytic enzymes, complexes of toxins and hemolysins; subsequently, the insects died during 24–72 h post-application (Ribeiro and Vaz 2019). Sometimes, EPNs can be applied in combination with insecticides without reducing their infectivity (Nishimatsu and Jackson 1998). All of these reasons contribute the EPN species to be more potency against FAW and IPM programs. Worldwide, many researchers have studied the efficacy of different nematode strains against *S. frugiperda* (Wattanachaiyingcharoen et al. 2021; Fallet et al. 2022), but till now very limited studies recorded in Egypt. Therefore, this study designed to assess the bioefficacy of 2 EPNs species (*Steinernema carpocapsae* (All) and *Heterorhabditis indica* (EGAZ2)) on different developmental FAW larval instars (2nd to 6th instars) according to different nematode concentrations and exposure times instead of chemicals. This study is the first against different larval instars of FAW in Egypt.

Methods

Culture of *S. frugiperda*

Initial culture of *S. frugiperda* larvae was collected from infested maize fields in Assiut Governorate, Upper Egypt. The insect rearing technique was conducted according to the methodology described by Mohamed (2022). FAW larvae were divided into plastic containers (25 cm diameter × 15 cm height) and fed on fresh maize leaves until pupation. Pupae were collected daily and placed on wooden rearing cages ($35 \times 35 \times 35$ cm^3) until adult moths' emergence. Moths were fed on (10%) honey solution hanged inside the cage and renewed daily. Newly laid eggs were collected daily, and neonates (F_1) were reared on fresh castor oil leaves (*Ricinus communis* L.) until pupation. Then, they were transferred to new cages for adult emergency and egg-laying. The FAW was maintained under laboratory conditions (27 ± 1 °C; > 60% RH and 12L: 12D) for 5 successive generations before the beginning of the experiments.

Entomopathogenic nematodes (EPNs)

Two nematode species, *Steinernema carpocapsae* (All) (Rhabditida: Steinernematidae) imported from Biosys Palo Alto, CA (USA) and *Heterorhabditis indica* (EGAZ2) (Rhabditida: Heterorhabditidae) isolated from Egyptian soil (Azazy et al. 2018), were tested against different larval instars of *S. frugiperda* to assess their efficacy. EPN species were supplied by Dr. Ahmed Azazy, Plant Protection Research Institute, Agricultural Research Center (ARC), Giza, Egypt, and were cultured in vivo on the full-grown larvae of the greater wax moth, *Galleria mellonella* Linnaeus (Lepidoptera: Pyralidae) as described by Shairra (2000). After inoculating, the emerged infective juveniles (IJs) from *G. mellonella* larval cadavers were collected in sterile distilled water (d. w.) using a modified White trapped by Kaya and Stock (1997) and were stored at 10 °C for *S. carpocapsae*, and at 15–20 °C for *H. indica* till needed. Freshly emerged IJs nematodes were kept at least 5 h at room temperature before usage in the experiments.

Pathogenicity bioassays and experimental design

For bioassay against FAW, 2nd to 6th healthy instars FAW larvae and different serial concentrations (150, 300, 600, 1200 and 2400 IJs/larvae/ml d. w.) were tested for

each nematode species. Six larvae from each instar/concentration/species were placed into plastic cups (7 cm height × 6 cm diameter) lined with a piece of napkin and castor oil leaves as larval food. A control treatment was conducted by placing tested instar larvae with castor leaves on the same volume of sterilized distilled water for each nematode's concentration. The larval food was added when needed, and the experiments were incubated under rearing conditions (27 ± 1 °C in full darkness). Three replicates/concentration/instar larvae for each nematode species and control were used in the bioassay experiment. After 48 h post-treatment, the larval mortality rates were checked in all tested cups and continued till full dead or completing their development and adult emergence. The larvae were marked as dead related to color change, odor and failure response to the forceps touch. In addition, LC_{50} (median lethal concentration) and slope were calculated for each nematode species at different concentrations.

Statistical analysis

One-way analysis of variance (ANOVA) was conducted to determine significant differences at the level of ($P \leq 0.05$) in all parameters of the experiment. Besides, two-way ANOVA was used to determine the effects of different concentrations and exposure time on the mortality rates of each larval instar in the two tested nematode species. The t test was carried out to determine a significant difference in the means between treatments ($P \leq 0.05$). Regression analysis was performed to determine a correlation between different experimental parameters and slope. Furthermore, LC_{50} estimation was performed using an online tool "Quest Graph™ IC_{50} Calculator", AAT Bioquest, Inc (https://www.aatbio.com/tools/ic50-calculator). All calculations and graphs were used by the Microsoft Excel® software (Fowler et al. 1998).

Results

Steinernema carpocapsae nematode against FAW larval instars

Based on the obtained results, 2nd instar FAW larvae were highly susceptible to infection by *S. carpocapsae* with 100% mortality after 48 h only, regardless the nematode concentrations (Fig. 1A). In 3rd instar (Fig. 1B), the full mortality rate was noted with the increase in IJs concentration (600–2400 IJs/ml) after 48 h of exposure, whereas the lowest concentrations (150–300 IJs/ml) caused mortality % about 44.44 and 83.33%, respectively, after the same time conditions (48 h), reaching 100% during 72 h post-exposure. Statistically, time exposure ($F_{1,8} = 2.898$; $P = 0.127$) and nematode concentrations ($F_{4,5} = 0.212$; $P = 0.921$) were non-significantly influenced the mortality rate of this instar larvae. In 4th and 5th developmental instars, mortality % was greatly increased related to IJs concentrations and exposure time ($P < 0.0002$) in comparable to the control treatment which recorded zero mortality (Fig. 1C, D). At 48 h post-treatment, the mortality % was the same value 66.67% at the highest concentration of 600–2400 IJs in the 4th instar (Fig. 1C), but decreased somewhat in the 5th instar larvae to (33.33–50%) (Fig. 1D). In contrast, the fully grown 6th instars were more tolerant, as all larvae died after 72 h of incubation at all tested concentrations (Fig. 1E). Based on our observation, the feeding behavior of all instars' larvae was very weak in all treatment after nematode exposure in comparable to control. As the developmental larvae increased, total mortality rate (100%) occurred after 72 h post-exposure. Hence, application of EPN, *S. carpocapsae* was more virulent against FAW larvae with different instars (Fig. 2). The overall mortality rates after nematode application were significantly varied based on FAW larvae with different developmental instars ($F_{4,40} = 19.626$; $P < 0.0001$), not by IJs concentrations ($F_{4,45} = 0.119$; $P = 0.995$). Therefore, direct relationships were found between the mortality rate and larval instar's development.

On the other hand, median lethal concentration values (LC_{50}) of this nematode species against different FAW larval instars were calculated (Table 1). Since the 100% mortality on the 2nd and 6th instars in all tested concentrations, LC_{50} values were not calculated. LC_{50} recorded the least values in the 3rd instar larvae (48 h; $LC_{50} = 170.415$; $P = 0.02$); followed by the 4th instar ($LC_{50} = 318.252$; $P = 0.01$), but the 5th instar was the highest one ($LC_{50} = 567.108$; $P = 0.656$). Besides, the nematode concentrations revealed a positive correlation with the mortality rate of all tested instars *S. frugiperda* larvae (Table 1).

Heterorhabditis indica nematode against FAW larval instars

The virulence effect of *H. indica* nematode was comparatively lower than *S. carpocapsae* and longer time required post-application to cause mortality against different instars, regardless the concentrations (Fig. 3). No mortality rates were observed in all tested instars with different nematode concentrations during the first 2 days post-exposure, with the only exception of the highest concentration (2400 IJs) that registered 20 and 12.5% mortality rates against the early instars of 2nd and 3rd larvae, respectively (Fig. 3A, B). In 2nd instar larvae, 100% mortality resulted after 96 h post-treatment at all concentrations (Fig. 3A). The accumulative mortality affected directly by time exposure ($F_{2,12} = 29.880$; $P < 0.0001$), not nematode concentrations ($F_{4,10} = 0.2005$; $P = 0.932$). In the case of

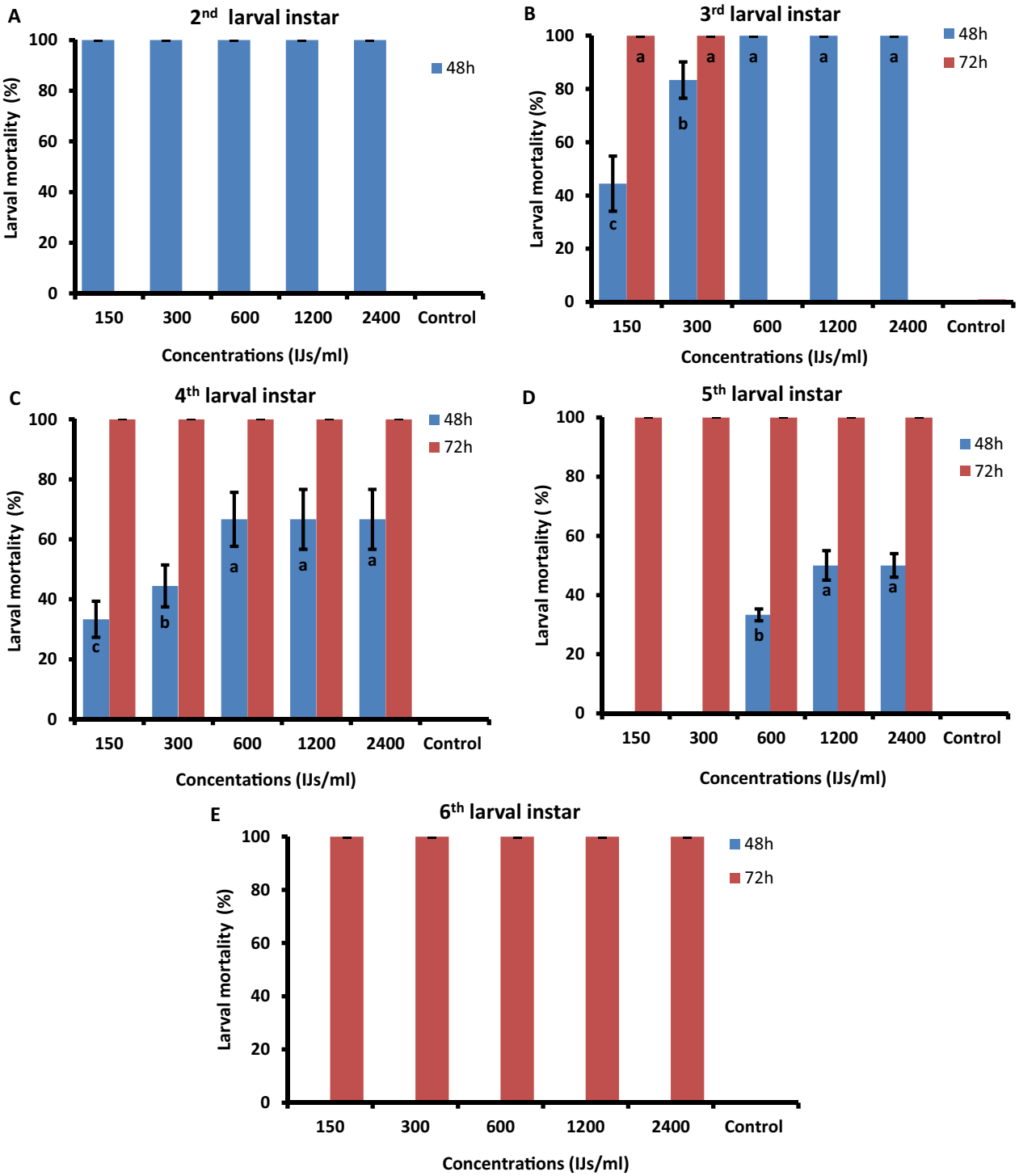

Fig. 1 Mortality percentages of different larval instars of *Spodoptera frugiperda* exposed to different infective juvenile nematode concentrations (IJs/ml) of *Steinernema carpocapsae*. Columns shared with the same letters within the same instar are statistically insignificant ($P > 0.05$)

3rd instar (Fig. 3B), the highest concentrations of 1200–2400 IJs after 72 h resulted in 42.86 and 14.28%, respectively, mortality rates, and all larvae died after 120 h post-treatment. However, lower concentrations of 150–600 IJs achieved 100% mortality after 96 h. Data analysis of this larval instar exhibited that the mortality rate was greatly influenced by time exposure only ($F_{3,12} = 20.395$; $P < 0.0001$), not the nematode

Fig. 2 Mortality of different larval instars of *Spodoptera frugiperda* after the application of EPNs, *Steinernema carpocapsae*

Table 1 Pathogenicity of *Steinernema carpocapsae* nematode against different larval instars of *Spodoptera frugiperda* at different concentrations (IJs/ml) after 48 h of exposure

Larval instar	LC_{50} (IJs/larva)	Slope ± SE	Coefficients (intercept)	R^2	Correlations	*P*-value
3nd instar	170.415	0.017 ± 0.012	72.219	0.296	0.611	0.020
4th instar	318.252	0.012 ± 0.007	51.389	0.484	0.696	0.015
5th instar	567.108	0.023 ± 0.009	5.554	0.675	0.822	0.656

LC_{50} values on the 2nd and 6th larval instar were not calculated as 100% mortality was caused at all tested concentrations

LC_{50} Lethal concentration kills 50% of FAW larvae

concentration rate ($F_{4,12} = 0.099$; $P = 0.981$). At 150–300 IJs concentrations and after 188 h post-exposure, the mortality rate achieved 100% in the 4th instar, and then, the time duration decreased gradually (164–120 h) as the concentration increased (Fig. 3C). The mortality directly varied in this instar by nematode concentrations ($F_{4,20} = 0.126$; $P = 0.04$) and time post-treatment ($F_{5,19} = 7.9112$; $P = 0.0003$). A further increase in FAW nematode concentration and time exposure ($P < 0.001$) resulted in a high mortality, particularly in the late larvae. At 150 IJs concentration, 50% only of the 5th instar larvae died after 96 h, and the same rate was after 188 h at 300 IJs (Fig. 3D). The survived larvae after infection were completed their development till pupation and adult emergence (Fig. 4). After that, FAW male moth appeared with slightly wing curled, but the female was with completely wing malformation than normal adults from the control and died without mating and/or egg-laying. Afterward, the first larval mortality was recorded after 96 h in the developed 6th instar at 1200–2400 IJs only and then reached to 100% mortality after 120 h, but after 188 h at 600 IJs (Fig. 3E). Contrary, lower concentrations (150–300 IJs) caused a moderate mortality ranged 33.33–50%, respectively, after 188 h post-incubation than other concentrations. The rest of larvae succeeded to survive after nematode infection was died in the pupal stage. The obtained results clarified that the effect of *H. indica* application on the overall mortality rate was greatly changed with different instar larvae (Fig. 5) ($F_{4,120} = 6.341$; $P < 0.0001$) and exposure time ($F_{5,21} = 5.607$; $P < 0.0001$) only. In this regard, the LC_{50} values for this nematode species against FAW developmental instars at different exposure periods were calculated (Table 2). At 72 h post-incubation, LC_{50} values were significantly increased as the instar larvae increased and valued 506.78, 713.776 and 2442.3 IJs/larva for the 2nd, 3rd and 4th instars, respectively. The lowest value of LC_{50} (27.616 IJs/larva) was calculated in the 4th instar after 120 h post-exposure and was 184.282 IJs/larva in the 5th instar after 96 h. However, LC_{50} was recorded only in the 6th instar for 164 and 188 h post-application compared to other instars.

Ultimately, the obtained results demonstrated that the larval mortality rate of FAW directly differed ($P < 0.0001$) by the application of 2 nematode species, *S. carpocapsae*

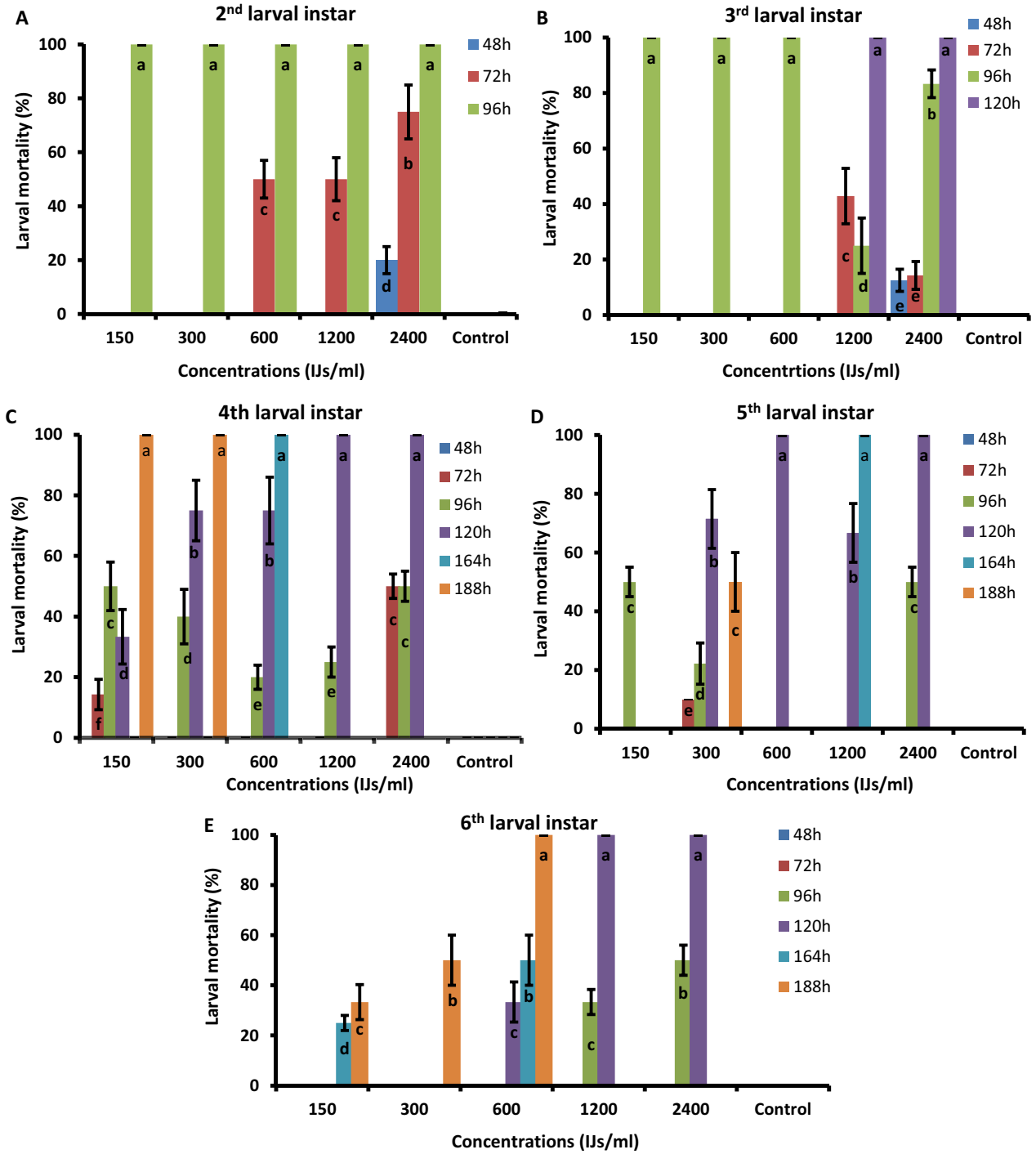

Fig. 3 Mortality percentages of different larval instars of *Spodoptera frugiperda* exposed to different infective juveniles nematode concentration (IJs/ml) of *Heterorhabditis indica*. Columns shared with the same letters within the same instar are statistically insignificant ($P > 0.05$)

and *H. indica*, developmental larval instars and post-exposure time ($P < 0.0001$), but not by the IJs applied concentrations ($P > 0.05$).

Discussion

There is an urgent need for minimizing the dependence of chemicals in pest control management. In this regard, biological control could be the promising strategy and environmentally safer than hazardous

Fig. 4 Larvae succeeded to complete their development after the application of *Heterorhabditis indica* at low IJs nematode concentration, showing male moth with slightly wing curled, but female with completely wing malformation

Fig. 5 Mortality of different larval instars of *Spodoptera frugiperda* after the application of EPNs, *Heterorhabditis indica*

chemicals for sustainable management of FAW (Akutse et al. 2019).

Many researchers have studied the efficacy of different nematode strains against *S. frugiperda* worldwide (Acharya et al. 2020; Wattanachaiyingcharoen et al. 2021; Fallet et al. 2022), and they proved that different strains caused mortality to FAW larvae, but with different rates and concentrations.

The present results revealed that the larval mortality rate of FAW varied significantly related to 2 tested

Table 2 Pathogenicity of *Heterorhabditis indica* nematode against different larval instars of *Spodoptera frugiperda* at different concentrations (IJs/ml) and exposure times

Larval instars	Exposure time (h)	LC_{50} (IJs/larva)	Slope ± SE	Coefficients (intercept)	R^2	Correlations	*P*-value
2nd instar	72 h	506.784	0.032 ± 0.01	5.208	0.763	0.874	0.05
3rd instar	72 h	713.776	0.011 ± 0.01	2.382	0.228	0.478	0.416
	96 h	756.681	0.013 ± 0.018	94.098	0.142	0.376	0.028
4th instar	72 h	2442.300	0.019 ± 0.008	4.4667	0.6187	0.786	0.115
	96 h	71.639	0.003 ± 0.001	34.375	0.034	0.185	0.049
	120 h	27.616	0.023 ± 0.01	55.554	0.580	0.762	0.027
5th instar	96 h	184.282	0.006 ± 0.01	18.749	0.050	0.581	0.717
	120 h	269.716	0.026 ± 0.02	43.453	0.338	0.581	0.304
6th instar	120 h	635.133	0.049 ± 0.004	1.388	0.776	0.881	0.048
	164 h	538.899	0.011 ± 0.012	25	0.193	0.440	0.458
	188 h	330.322	0.151 ± 0.014	8.33	0.992	0.996	0.05

nematode species, post-exposure times and developmental instar larvae. Besides, *S. carpocapsae* nematode application was more virulent and potency against all FAW instars, achieving 100% mortality during 48–72 h post-exposure. These findings were in accordance somewhat with Fallet et al. (2022) who cleared that Rwandan *S. carpocapsae* strain (RW14-G-R3a-2) caused rapidly 100% mortality in 2nd and 3rd instars, but the rate decreased somewhat to 75% in 6th instar. Besides, (Sayed et al. 2022) recorded that the highest mortality rate 100% was in the 3rd and 5th instars larvae after 3–4 days of irradiated *S. carpocapsae* infection and was 72.2 and 77.8%, respectively, for the tested instars with un-irradiated strains. Also, (Acharya et al. 2020) reported *S. carpocapsae* were highly potential against younger larvae (1st–3rd) only, while other strains as *S. arenarium* and *S. longicaudum* were against older ones (4th–6th). Additional support study by (Caccia et al. 2014) that confirmed 50–100 IJs of *S. diaprepesi* caused 93–100% mortality rates in the FAW last instar larvae after 144 h. Contrary, *S. riobrave* was poorly effective against FAW larvae, even at high concentrations (Andaló et al. 2010).

On the other hand, FAW early instars were highly susceptible to *H. indica* infection and this obtained result was agreeable with that observed previously by (Acharya et al. 2020; Lalramnghaki et al. 2021; Shinde et al. 2022). In confirmation to these findings, the lower nematode concentration against late larvae (5th and 6th instars) in our study caused lower mortality ($\leq$ 50%); subsequently the recovery larvae after infection completed their development till pupation and/or adult emergence with wing deformation. This concept was in consistence somewhat with other tested nematode strains as studied by Fallet et al. (2022) that different EPN strains did not affect negatively the survival of FAW pupae at (5, 25, 125 IJs/larvae). However, Acharya et al. (2020) reported about 67% reduction in the FAW emergence rate after 5 days of exposure to 600 IJs of *S. carpocapsae*.

Obtained results also clarified the superiority of *S. carpocapsae* nematode over *H. indica* in all tested FAW instars, regardless the IJs concentrations. This finding was supported by many other studies that confirmed Steinernematidae genera which is highly effective as a biocontrol agent against different *Spodoptera* spp. and among them *S. frugiperda* (Archarya et al. 2020; Fallet et al. 2022; Sayed et al. 2022). These differences in virulence and infectivity between Steinernematidae and Heterorhabditidae may be related to the host insect specificity, morphological features of nematode strains and their tolerance to host-immune responses (Elbrense et al. 2021).

Ultimately, the variations in the susceptibility and mortality rates among developmental instars' larvae may be related to their morphological structures, sizes, behaviors and immune defense mechanisms as suggested previously by (Elbrense et al. 2021). Besides, the reproduction rate of EPNs has been influenced directly by different developmental stages of the host insects (Park et al. 2001).

Conclusion

Pathogenicity bioassays of the 2 nematode isolates species, *S. carpocapsae* (All) and *H. indica* (EGAZ2), against FAW larval instars confirmed that both species were able to infect and cause mortality in all tested instars, but with different rates and exposure times. Indeed, *S. carpocapsae* was more virulent and effective than *H. indica*, achieving 100% mortality after 48 h in early instars, and 72 h in late instars, under laboratory conditions. In contrast, application of *H. indica* registered 100% mortality

on the late instars after (120–188 h) at the highest concentrations only. Therefore, these EPN species could be highly recommended as promising biocontrol agents against this invasive FAW for sustainable agriculture, based on the achieved results, especially *S. carpocapsae.* Further experiments on the EPN application should be evaluated under field conditions.

Abbreviations

FAW	Fall armyworm
EPNs	Entomopathogenic nematodes
IJs	Infective juveniles
h	Hour
d. w.	Distilled water
LC_{50}	Median lethal concentration

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Author contributions
HOM and SAS designed and planned the experiments. HOM conducted all the experiments, wrote the manuscript, analyzed the data and edited the final draft. SAS revised the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
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Declarations

Ethics approval and consent to participate
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Consent for publication
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Competing interests
The authors declare that they have no competing interests.

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