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Role of Mermithid Nematodes in the Management of Agricultural and Household Insect Pests: A review

Deepak Kumar, Pinki Nagal, Harjot Singh Sidhu, Puneet Ranga, Pritam Kumari

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ABSTRACT

The increasing challenges associated with using chemicals in managing agricultural and household insect pests has prompted a re-evaluation of previous approaches and the search for new ones as alternatives or supplements to the present management programmes. The introduction and release of bio-agents, like fungi, bacteria, viruses, nematodes, and insects for the control of pests is a novel biological control strategy. Among bio-agents, the role of mermithid nematodes in insect-pest management has been considered. Mermithids are prime candidates for biocontrol of insects due to their adaptability to the life cycle of the host, a high degree of host specificity often limited to one or more species of insects, high reproductive potential, free swimming behavior making dissemination of pre-parasitic stage easy, pathogenic ability and high levels of parasitism. Another useful trait favoring their employability is their non-feeding habit soon after emerging from the host body, making their handling simple. The morphological, physiological, and behavioral responses of host insects are significantly disrupted by mermithid infective juveniles often the J2 stage. Many mermithid infections cause abdominal distortion, discolored cuticle/integument, and a decrease in total fat body content of the host. The parasitism by these nematodes can lead to formation of intersexual conditions in the host insects which also create distortion to endocrine system. Owing to such mechanism of parasitism of mermithids, these nematodes are one the best considerations as bio-control agents.

Keywords Mermithids, Pest management, Parasitism, Biological control.

Deepak Kumar[1], Pinki Nagal[2], Harjot Singh Sidhu[3]*, Puneet Ranga[4], Pritam Kumari[5]

[1,3]Assistant Professor, [4,5]PhD Scholar
Department of Nematology, MPUAT, Udaipur- Rajasthan 313004, India

[2]CDLU, Sirsa, Haryana 313004, India

[3]Nematology, MHU-Regional Mushroom Research Station, Murthal, Sonipat, Haryana 131039, India

[4,5] Department of Entomology, CCS HAU, Hisar, Haryana, India

Email: hss.apn@mhu.ac.in
*Corresponding author

INTRODUCTION

There are various nematodes in our surrounding which are obligate/facultative parasites of various soil borne pathogens, insects, spiders, scorpions, crustaceans, earthworms, leeches, and molluscs. The nine most important nematode families viz., Allantonematidae, Diplogasteridae, Heterorhabditidae, Neotylenchidae, Mermithidae, Rhabditidae, Sphaerulariidae, Steinernematidae, and Tetradonematidae include nematode species capable of attacking, killing, and inducing sterilization in insects or altering the growth of their host. Mermithids are parasitic nematodes belongs to phylum Nematoda which are generally translucent white, thin, and cylindrical in shape. Mermithid group of worms are generally confused with the horsehair worms grouped under phylum nematomorpha due to similar outlook and life history. The nematodes belonging to the family mermithidae are endo-parasitic in arthropods. More than 25 species of mermithids are found parasitic on mosquito larvae and all this making these nematodes as bioagents for mosquito control (Platzer 1981). Mermithids vary in length ranging from 10-100 mm and are easily detectable in host insects simply by dissection or when they leave their hosts. A species of mermithidae family, *Pheromermis vesparum* was found parasitic on *Vespa velutina* (invasive Asian hornet) in France.

Generally, mermithids have two types of life cycles- direct and indirect. Some mermithids that have close association with aquatic insects belonging to order Diptera (Chironomidae, Ceratopogonidae and Culicidae) exhibit a direct life-cycle in which the juveniles tend to complete their entire growth and development within the host body and later emerges from the host insect cadaver (Fig. 1). The juveniles soon after emergence from the host, molts into adult, mates and starts laying eggs in the environment of host. The infective juveniles on hatching from eggs locate for the host by active body movements and enter host body through natural openings or wounds, if any. In indirect life-cycle, an intermediate host often referred to as the paratonic host is needed to complete the life-cycle. The paratonic host (often an invertebrate) ingests the eggs laid in the host environment, ingests them and the juveniles emerge within the gut, penetrate the gut wall entering the hemocoel. The juveniles then undergo a diapause stage in encysted condition allowing the host to continue its life cycle. On completing the growth phases within the host body, the juveniles then emerge from the host leaving the cadaver behind (Poinar 2012).

Fig. 1. Dead mosquito larva with post-parasitic nematode emergence (Abagli *et al.* 2019.

Mermithids fit well in biological control programs due to numerous attributes such as ease of application, safety to environmental, host-specificity, ease of mass multiplication under laboratory conditions and their effectiveness or lethality to a wide range of hosts (Petersen 1985, Kerry and Hominick 2002). Numerous studies have been conducted in order to describe the potential bio-control of aquatic and terrestrial insect-pests illustrating the potential scope encompassed by these mermithid species in biocontrol programs.

Important species of Mermithids

Nematodes occurring in mermithidae family are generally considered as parasites of terrestrial as well as aquatic vertebrates (Table 1). Dujardin 1842 first described the genus Mermis based on description of type-species *M. nigrescens* Mermis was subsequently considered to be as a nominal genus for all nematodes

Table 1. The important genera of the family Mermithidae:.

Sl. No.	Name of Genera
1	*Abathymermis* Rubtsov 1871
2	*Aranimermis*
3	*Cretacimermis* Poinar 2001
4	*Eumermis* Daday 1911
5	*Gastromermis* Micoletzky 1923
6	*Heydenius* Taylor 1935
7	*Hydromermis* Corti 1902
8	*Lanceimermis* Artyukhovskii 1969
9	*Mermis Dujardin* 1842
10	*Quadrimermis* Coman 1961
11	*Reesimermis* Tsai and Grundman, 1969
12	*Romanomermis*
13	*Spiculimermis* Artyukhovskii 1963
14	*Strelkovimermis* Rubzov 1969
15	*Tetramermis* Steiner 1925

Table 2. Important species included in the genus Mermis:.

Sl. No.	Name of species
1	*Mermis athysanota* Steiner 1921
2	*M. changodudus Poinar, R*emillet and Van Waerebeke 1978
3	*M. gigantean* Artyukovsky and Lisikova, 1977
4	*M. kenyensis* Baylis, 1944
5	*M. mirabilisvon* Linstow, 1903
6	*M. nigrescens* Dujardin, 1842
7	*M. papillus* Gafurov, 1982
8	*M. paranigrescens* Rubstov, 1976
9	*M. quirindiensis* Baker and Poinar, 1986
10	*M. savaiiensis* Orton Williams, 1984
11	*M. xianensis* Xu and Bao, 1995

that we would be characterized as mermithids (Table 2). More than 100 species have been identified and placed under the genus Mermis, a large fraction of which were published before 1950. As much as 20 species among the described species have been placed under different genera, but many species are yet to appear under the Mermithid group awaiting the re-examination of original type specimens (Table 3) (Presswell *et al*. 2013).

Host range of Mermithids

Mermithids have a broad host range encompassing as much as 12 genera of invertebrates, mainly Diptera and Hemiptera with variable habitats i.e., terrestrial as well as aquatic. The mermithids were earlier not found to parasitize aphids as their entry to insect body via. Mouth parts were difficult (Poinar, 2017), aphid infection by nematodes, *Caulinus burmitis* (Hemiptera: Burmitaphididae) by a fossil mermithid is one such record. Some unidentified mermithids are also reported to be associated with aphids i.e., nymphs and winged adults of the root aphids in Italy. Recently, the winged females of gall forming aphids, *Erisoma auratum* and *Tetraneura radicicola* were found to be targeted by the mermithid associated with leadplant, Amorpha canescens, which is the first such report of its kind (Tong *et al.* 2021). *Mermis nigrescens* (a notable parasite of grasshoppers) is reported to be associated with several other insects like Dermaptera (earwigs), Coleoptera (beetles) and Lepidoptera (moths and butterflies). Host physiological conditions have a great impact on the growth, development, and survival of associated mermithid parasites. Insect

Table 3. Global host records of Mermithids (Martins *et al.* 2020).

Mermithid genera	Host species	Location	References
	Chinavia hilaris (Say 1831)	United States	Stubbins *et al.* 2016
	Euschistus servus (Say 1832)	United States	Stubbins *et al.* 2016
Agamermis	*Euschistus* sp.	United States	Stubbins *et al.* 2016
	Megacopta cribraria (Fabricius 1778)	United States	Stubbins *et al.* 2016
	Euschistus spp.	United States	Stubbins *et al.* 2016
	Sogatella furezfera (Horvath 1899)	Asia	Choo and Kaya 1993
	Acrosternum hilare (Say 1832)	United States	Kamminga *et al*. 2012
	Euschistus servus (Say 1832)	United States	Kamminga *et al.* 2012
	Aelia rostrata Boheman 1852	Turkey	Tarla *et al.* 2012
Hexamermis	*Chinavia hilaris* (Say 1831)	United States	Kamminga *et al.* 2012
	Eurygaster integriceps Puton 1881	Turkey	Memişoğlu *et al.* 1994
	Halys dentatus (*Fabricius* 1775)	India	Dhiman and Yadav 2004
	Platynopus sp.	India	Gokulpure 1970
	Piezodorus guildinii (Westwood 1837)	United States	Kamminga *et al*. 2012
	Rhaphigaster nebulosa (Poda 1761)	Italy	Manachini and Landi 2003
	Aelia rostrata Boheman 1852	Turkey	Memişoglu *et al.* 1994
Mermis	*Eurygaster integriceps* Puton 1881	Turkey	Dikyar *1981*
	Piezodorus guildinii (Westwood 1837)	Uruguay	Riberiro and Castiglioni 2008
Pentatomermis	*Coptosoma mucronatum* Rubostov 1977	Slovakia	Rubtsov 1977
	Elasmostethus interstinctus (Linnaeus 1758)	Russia	Rubtsov 1969
	Nezara viridula (Linnaeus 1758)	India	Bhatnagar *et al.* 1985
Unidentified	*Aelia acuminata* (Linnaeus 1758)	Uzbekistan	Sultanov *et al.* 1990

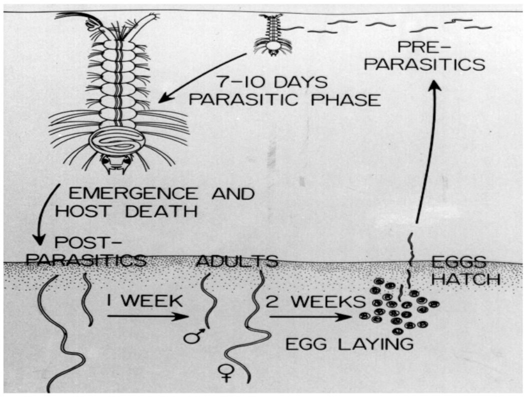

Fig. 2. Life cycle *Romanomermis culicivorax.*

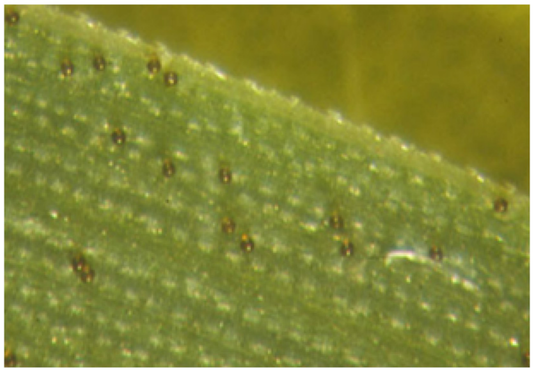

Fig. 3. Eggs of *Mermis nigrescens* (grasshopper nematode) Photograph by John Capinera, University of Florida.

parasitic nematodes derive the nutrition required for their growth, development and reproduction from the host tissues and hemolymph, in particular (Mcrae *et al.* 2015).

Biology and life cycle of Mermithids

Aquatic mermithid: *Romanomermis culicivorax*

Nematodes are capable of surviving and swimming in water in order to seek a suitable host for up to 48 hrs. Second stage juvenile is the parasitic stage of these nematodes and can last slowly for the first three or four days. Total life cycle is completed in 3-8 weeks based on ambient temperature conditions or it may extend or lessen based on environmental conditions. Fecundity depends mainly on the species, like a female of *R. culicivorax* can lay about 2500 eggs over an egg laying period of 10-15 days (Fig. 2).

Terrestrial mermithid: Mermis nigrescens

After completing the growth, juveniles enter the soil by leaving their host up to a depth of 20-40 cm based on moisture status. Soon after mating, females instead of laying eggs, retain the eggs in the uterus for embryonic development to take place. Additionally, a layer is also deposited over them to provide protection against dehydration. For adhering to dry vegetation, the egg surface has rows of polar hairs for adhesion (Fig. 3). When grasshopper feed on vegetation, ingests the eggs of mermithids which later hatch out in the gut of grasshopper. The juveniles can remain in the gut of host for about 4 to 10 weeks growing up to 9-15 cm in length (Fig. 4).

Terrestrial mermithid: *Amphimermis* spp., *Agamermis* spp., *Hexamermis* spp.

These nematode species have much similarity in life cycle as compared to the Mermis spp., differing only in the mode of laying eggs as in these species the females leave the soil to lay eggs on vegetation. The eggs later hatch and juveniles (J2) tend to seek hosts for infection to bore via body wall.

Mating in mosquito parasitic nematode, *Strelkovimermis spiculatus*

After the parasitization, females of mermithids drive formation of mating clusters and attract males. Molt-

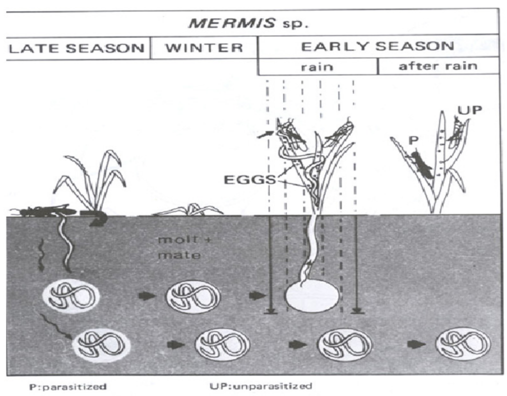

Fig. 4. Life cycle of *Mermis nigrescens.*

ing of female adults trigger the mating behavior of males. Before mating initiation, the male coils its tail around the adult female's cuticle and migrates along the female near the molting cuticle until the vulva is accessible and mating can take place. Because of his intermediate location between the vulva and later arriving males, the first arriving male is guaranteed access to a virgin female. Before departing the female, male deposit an adhesive gelatinous copulatory plug into and over the vulva. Larger mating clusters had higher fecundity, although this was due to a faster rate of molting, which is required for mating. The mermithid system, which is relatively simple to cultivate and manipulate, could be used as a model for experiments on male–male confliction, protandry, penile erection hooks and female selection in coupling clusters (Dong *et al.* 2014).

Host-Parasite Relationships

Mermithid infective juveniles cause significant disruption in the morphology, physiology, and behavioral responses of the various host insects. Many mermithid infections cause abdominal distortion, discolored cuticle/integument, and a decrease in total fat body content in the host. Sometimes, the infection leads to arrested development of host's larval, pupal and adult stages upon parasitization and can also prevent metamorphosis. Inhibition of pupation associated with parasitism is probably a symptom of severe nutrient depletion rather than an active alteration of the black fly's hormonal system by the infective juveniles (Condon and Gordon 1977). So, the parasitized larval stages of flies that do pupate or emerges, are usually sterile due to incomplete development of their reproductive systems. Some reports stated the degeneration of the nervous as well as digestive systems in parasitized adult hosts (Hocking and Pickering 1954). In Simulium damnosum, the ovarian development was inhibited in almost 99% of infected adults and these flies lived only half as long as non-parasitized females (Mondet *et al*.1976). Mermithid parasitism can lead to formation of intersexual adults in black flies which also create disturbance to endocrine system in host insect (Rubtsov 1958). Females in mosquitoes have a high affinity towards the source of bloodmeal than to water, whereas the adult females parasitized by mermithids have high tendency to look for a water source 2-3 times more than source of a bloodmeal. This is the behavioral change brought in by the parasitic nematodes in its host to ensure advantage in survival, better chances of host finding and ultimately on the dispersal (Campos and Sy 2003).

It is still unclear whether the parasites have an adverse influence on offspring wellness by directly competing for nutrition or by prenatal changes brought in the host by them. In order to investigate host manipulation by mermithid nematodes in future studies, several mechanisms underlying the changes in physiology need to be deciphered along with the signaling mechanisms and pathways governing them at the molecular level.

Boo-efficiency of Mermithids

The intensive use of chemical pesticides against various agriculturally and household important insect pests has led to the development of widespread pesticide resistance. So, the mermithid nematodes can be one of the several natural control alternatives to synthetic pesticides for insect pest suppression. Various studies have been conducted to evaluate the efficacy of these nematodes for control of harmful pests.

Orthoptera

Early studies on mermithid parasites of agriculturally important insects were mainly focused on grasshoppers which is a common host for *M. nigrescens* and *A. decaudata* (Cobb *et al.* 1923). In the spring, after rainfall or during periods of heavy dew, *M. nigrescens* females, which are around 8 cm in length, emerge from the soil and crawl over the existing vegetation to lay their eggs. Grasshoppers grazing on the foliage may subsequently consume the eggs which upon ingestion clump together in insect's intestine and likewise these pre-parasites make their way into the body cavity of host (Fig. 5). Mermithids species are believed to be crucial in not only management of grasshopper but *A. decaudata* also parasitized new hosts in nature like long-horned grasshoppers, crickets, wolf spiders and leafhoppers (Nickle 1981). Grasshoppers when infected with *Mermis* spp., the fecundity was altered. Infested insects produced 17.53, 11.25 and 8.64 eggs per female, respectively,

Fig. 5. Parasitic juveniles of Allomermis solenopsi infecting fire ant worker (Poinar *et al*. 2007).

for *Poekilocerus pictus, Oxya velox* and *O. hylahyla,* whereas uninfected grasshoppers produced 43.35, 37.86 and 39.34 eggs per female, respectively. In addition, it was discovered that insects infected with *Mermis* spp. did not live long. Oocyte and testis development were significantly suppressed in infected individuals, according to investigations including dissection of cadavers (Riffat *et al.* 2018).

Hemiptera

Among the pentatomid species, the brown stink bug, Euschistus servus (Say), the green stink bug, Chinavia hilaris (Say) and the southern green stink bug, *Nezara viridul*a (L.), are the most important agricultural pests in most nations (Greene *et al.* 2001). During 2014, the stink bugs contaminated 2.5 million hectares of cotton, *Gossypium hirsutum* L., causing $106 million in damage and ruining 135,000 bales in the United States (Williams 2015). These species not only attack cotton crop but cause serious damage to soybean (*Glycine max* L.), peach (*Prunus persica* L.), tomato (*Solanum lycopersicum* L.), sorghum (*Sorghum bicolor* L.), wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.). The mermithids, *Hexamermis* spp., *Agamermis* spp., *Mermis* spp. and *Pentatomermis* spp. are found associated with these insects and observed as effective biocontrol agents in United States, India and Turkey (Dhiman and Yadav 2004, Tarla *et al.* 2012).

Diptera

In West Africa, malaria mosquito larvae were found susceptible to *R. iyengari* infection. The severity of parasitism is determined by the concentrations of nematodes tested. In wetlands and flood-prone areas in West Africa, a monthly application of 3500 J2/m^2 was adequate to effectively reduce larval Anopheles gambiae (Figs. 6, 7, 8) (Abagli *et al*. 2019). The nematode, Pheromermis pachysoma is a potent biocontrol agent for wasps (Vespula pensylvanica) in places of USA where these invasive wasps pose serious threats to economy, society and ecosystems (Villemant *et al.* 2015). The wasps when subjected to various levels of nematode infection during colony formation phase, were predicted to have the greatest impact on lowering sexual function (Martin 2004).

Coleoptera

Mermithids are also known to be parasitic on beetles that feed on leaves and roots. *Psammomermis* spp. infected 60% of Japanese beetles in parts of the Soviet Union. Mazza *et al.* (2017) discovered a similar mermithid nematode parasitizing Japanese beetle, Papilio japonica grubs from lawns in the northeastern

(Photograph by John Capinera, University of Florida)

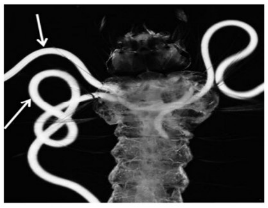

Fig. 6. Mature juvenile of *Mermis nigrescens* leaving grasshopper cadaver. **Fig. 7.** *Romanomermis iyengar*i post-parasites exiting from the host anterior prothorax (Sanad *et al.* 2013). **Fig. 8.** Emergence of *Strelkovimermis spiculatus* (arrow) between the anal gills and anus (Sanad *et al.* 2013)

United States. The nematode is about 20 cm long and coiled within the insect, spanning from the thoracic region to the pre-ultimate abdominal segment. Mermithid infected 60% of the grubs gathered from sandy soil on the town green in Brattleboro, Vermont. *Hexamermis arvalis* parasitized up to 33% of alfalfa weevils in portions of New York (Poinar and Gyrisco 1962). Blaxter and Koutsovoulos (2015) found that a nematode termed Filipjevimermis leipsandra parasitized 50-100 per cent of the banded cucumber beetle larvae taken from farms in Charleston, South Carolina (Poinar and Welch 1968). Most of the insects parasitized by this nematode died before pupating, as is expected. When the mermithids emerged, 86% of the 219 insects were last-instar larvae, 6% were prepupae, 7% were pupae and 1% were adults. Infected larvae swelled slightly and took on a distinctive light tan color. They were lethargic and clumsy in their movements and well-developed mermithids were also visible through all the integument.

Lepidoptera

Caterpillars and other larval lepidopterans found infected with mermithids. From New Jersey to Virginia, *Hexamermis* sp. was reported parasitizing tent caterpillars on *Prunus* sp. *Hexamermis* mermithid nematode was used to infect the fall armyworm (Nickle 1978). It was quite astonishing that the infective stage, which was about 1 mm long, developed inside the armyworm caterpillar to a post-parasitic nematode 20 cm long within 20 days period. Nickle and Grijpma (1974) found that up to 25% of the shoot borers, *Hypsipyla grandella* (Zeller) (Pyralidae), were infected by *Hexamermis albicans*. They also reported, more than 70 species of Lepidoptera order to be parasitized by mermithids.

Among the lepidopterans, *Amyna axis* (Family: Erebidae), *Chrysodeixis acuta, Chrysodeixis eriosoma, S. exigua* and *S. litura* (Family: Noctuidae) are major polyphagous insect-pests reported to be parasitized by mermithid (Nematoda: Mermithidae) nematodes in the regions of Rajasthan. The nematode is believed to be member of the genus Hexamermis, based on the morphological and molecular evidences. This was arguably, the first such report of natural parasitism of *A. axis, Chrysodeixis* spp. (Fig. 9) and *Spodoptera* spp. (Fig. 10) by mermithids along with its molecular characterization from Rajasthan (Babu *et al.* 2019).

Fig. 9. Dead larva of *Chrysodeixis acuta* due to infection by *Hexamermis* sp.

Strengths

When compared to chemical insecticides, biological control with mermithids has numerous advantages in a pest management. One of the most significant benefits is that entomophilic nematodes are non-polluting and do not introduce pollutants into the environment. Another significant advantage of mermithid is its selectivity. Significant damage to non-target species can lead to a reduction in the population of natural enemies, selectivity is the most important factor in agricultural ecosystem balance (Kok and Kok 1999). Non-target species are only at a low risk of being harmed in this manner. Tebit (2017) emphasized that, unlike conventional pesticides, such practices of nematode use do not create new problems like ill-effects

Fig. 10. Dead larva of *Spodoptera litura* due to infection by *Hex*.

on non-target organisms including the vertebrates (Emden 2004). Other advantage of these nematodes, is their ability to self-replicate in host itself. This is critical in terms of the economic viability of these bio-agents. The insect-pest/host is unable (or takes a long time) to develop resistance against mermithids (Tebit 2017). However, it is likely that a target pest can develop defense mechanisms against an attack by a natural enemy. For instance, we could assume that efficient pest management by an entomophilic nematodes would result in selection pressure on the pest to establish escape mechanisms or tolerance to regulate agent attacks, thereby breaking down the biological control system (Holt and Hochberg 1997). Furthermore, this method can be cost effective. Its effectiveness is dependent on self-perpetuation and self-propagation, as previously stated. As a result, establishing a control agent in a particular location will decrease the desired pest to an acceptable limit for a longer length of time (Kok and Kok 1999). Handful of such nematodes can multiply to very high population densities as well as provide consistent pest control over a large area. When the cost of deploying nematodes is considered, biological control is generally less expensive than chemical control. When there are no other options, such as inaccessible areas, the financial benefit of biological control is greatest.

Constraints

In most cases of biological control programs utilizing such nematodes are harder to execute and maintain due to extreme unfavorable climatic conditions. The main drawback of these nematodes is the risk associated with income stability of agricultural crop. Furthermore, they seem to be more vulnerable to environmental factors than agrochemicals. As a result, pest population fluctuations occur which generally not acts as continuous host for nematodes. The other major issue is that it is incompatible with agrochemicals. According to Emden (2004), such nematodes restrict the subsequent use of agrochemicals because “where bio-agents are used against one pest, it is obviously difficult to sustain using insecticides against other pests on the same crop or other disease vectors in the same area.” This may make the use of these mermithids slight impossible in pest management system. Furthermore, these nematodes have a slow onset of action and does not result in rapid control. These will take a few days, if not weeks, for mosquito populations to be significantly reduced in size (Mullen and Durden 2002). It necessitates highly qualified or skilled scientific personnel to deal with these tiny worms which is difficult to maintain and handle and sometimes costly to develop (Tebit 2017).

CONCLUSIONS

Generally, various approaches have been practiced in insect pest management. In one or other way, these practices abort or do not fulfill the aim of pest management. As, chemical method is avoided due to their pollutants and ill-effects on human health also, biological control should be adopted by the farmers and even by the resident peoples in their surroundings to control the mosquitoes, crickets etc. Furthermore, chemical insecticide-based mosquito control fails due to environmental variances and variations in the behavioral characteristics of many mosquito species leads insecticide resistance among mosquito strains and pest resurgence. As a result of these reasons, there is great need to adopt various bio-agents which grows and develop naturally in habitat. So, keeping these all points and efficiency of mermithids against various insect-pests like grasshoppers, crickets, ants, mosquitoes, lepidopteran insects etc. this review has been designed.

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