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Review on ecology of entomopathogenic nematodes

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Abstract
Entomopathogenic nematodes mainly have symbiotic association with gram positive bacteria *Xenorhabdus* spp. and *Photorhabdus* spp. Entomopathogenic nematodes (EPNs) are beneficial nematodes parasiting insect pests and are being effectively used as a bio pesticide against a wide variety of insect pests. The abiotic and biotic factors affect the activity of entomopathogenic nematode showing differential response with different nematodes. The survival, infectivity, development and reproduction of entomopathogenic nematodes adversely affected when exposed to unfavourable environmental conditions.

Keywords: Entomopathogenic nematodes, insect pest, biocontrol agents, ecology

1. Introduction
Entomopathogenic nematodes (EPN) of the genera *Steinernema* and *Heterorhabditis* (Nematoda: Rhabditida) are effective biocontrol agents against insect pests, such as sciarid flies, weevils, scarab grubs, thrips, mole crickets and many lepidopteran pests whose pathogenicity is partly due to their symbiotic association with bacteria of the genera *Xenorhabdus* and *Photorhabdus*, respectively [1]. EPN were first applied to control Japanese beetles in the 1930s, and since the 1980s have been applied in inundative biological control programs to control several important insect pests [2]. The infective juveniles (IJs) actively seek out insects in the soil. The IJs enter the insect through the natural openings and, in the case of *Heterorhabditis*, through the cuticle. In the insect hemocoel, the IJs release their symbiotic bacteria from their gut, resulting in insect death. Following development to adult stages, reproduction produces thousands of fresh IJs, which emerge into the soil from the host insect cadaver. The abiotic constituents of soil *viz*., aeration, moisture, temperature, humidity, texture, structure affect the function of entomopathogenic nematodes, where various nematodes respond differently to the soil components [3]. Environmental parameters such as moisture, temperature and UV radiation influence short and long-term persistence of entomopathogenic nematodes is important for predicting the fate of nematodes to release as biocontrol agents. Entomopathogenic nematodes are not effective at high temperatures, because they are highly sensitive to UV light and require adequate moisture and high relative humidity for survival, virulence and effectiveness to a considerable period of time [4].
The prevalence and intensity of EPNs can vary with time, crop grown and soil type [5]. Factors influencing the motility and survival of infective juveniles are soil moisture, temperature, soil texture, soil pH and biotic factors [6]. The activity and survival of the entomopathogenic nematodes is greatly influenced by the prevailing temperature and moisture conditions [7, 8]. The low range of temperature tolerance is a limitation in their wide scale use in agriculture especially in subtropical and tropical countries like India, where temperature in plains vary from 10° to 45 °C. The *Steinernematidae* may survive at temperature range of 4° to 30 °C whereas *Heterorhabditis* survive at optimum range of 15° to 28 °C.

2. Abiotic factors affecting Entomopathogenic nematodes
Among the different abiotic factors, temperature, moisture and ultraviolet radiation play an important role on the efficacy of entomopathogenic nematodes.

2.1. Effect of temperature
Temperature is one of the important factors affecting both entomopathogenic nematodes and their symbiotic bacteria. Entomopathogenic nematodes are not effective at very low and high temperature.

The various processes such as host penetration, infection, development and reproduction by the nematodes and ultimately the biocontrol efficacy against insect pests are great influenced by temperature.

Temperature is an important factor in the life cycle of entomopathogenic nematodes [9]. Varying temperatures have effects on the viability of the IJs and their ability to reproduce, these effects are observed mainly in extreme temperatures (0 and 40 °C), which are lethal [10-12]. Soil temperature can have a great effect on nematode activity [13]. Optimum temperatures for infection and reproduction vary among nematode species and strains [14, 12, 15] report that at temperatures below 15 °C infection is not good, while at temperatures between 15 and 35 °C infectivity is optimal. In the case of *Heterorhabditis* sp. SL0708, greatest infectivity is presented at 20 °C, diverging from results found by [12] for some species of Heterorhabditidae, where 25 °C was the optimum temperature or 30 °C for *Heterorhabditis georgiana* [16]. The inconsistency in results regarding temperature for different species of the *Heterorhabditis* genus, shows that a single temperature cannot be assigned to the genre and that the infectivity of nematode species may also depend on the size of the larva, the depth of the host in the substrate and search behaviour of the IJs [17, 11].

Steinernema carpocapsae was able to kill *Galleria mellonella*at 13 ºC when the nematode was injected into the host haemocoel [18-21] observed the mortality of *G. mellonella* larvae by *S. carpocapsae* at temperatures ranging from 10º to 32 ºC and concluded that the death of larvae occurred more quickly at higher temperatures. Development of *S. carpocapsae* was favourable neither under very low (10 ºC) temperatures either high temperature (33 ºC) [22]. It was observed that though the bacterial symbiont had the maximum growth at the temperature range of 30º-33 ºC, the optimum temperature for the development of *S. carpocapsae* was 25 ºC [20, 23] Conducted studies on influence of temperatures and dosage on the mortality of larvae of *G. mellonella* caused by *Heterorhabditis bacteriophora.* The larvae of *G. mellonella* were killed by *H. bacteriophora* and its bacterial associate *Photorhabdus luminescens* at temperatures ranging from 12º to 28 ºC. The nematode's development was inhibited at both 12 and 30 ºC. But the bacterium reproduced and caused mortality from 12º and 33 ºC. [24] Reported that even at low temperature of 9 ºC *S. carpocapsae* caused host mortality but takes longer period of time (312 h) while only 16 h was taken for causing host mortality at 30 ºC. [7] That most of the *Steinernema* species did not develop and reproduce at temperatures higher than 27 ºC. [25] Observed significant differences between the three isolates of *Heterorhabditis* sp. (H181, Hf85 and Hnh186) from the Netherlands in respect of the number of infective juveniles that entered the larvae of *G. mellonella* at 9 ºC and 12 ºC. At 9 ºC penetration of Hf 85 was significantly higher than the other two isolates. Very few infective juveniles of Hf 85 penetrated at 7 ºC and parasitisation ceased at 5 ºC. [26] four isolates of *Heterorhabditis* sp. *viz*., H181, Hf85 and Hnh186 from the Netherlands and K122 from Ireland in the laboratory bioassays, where *G. mellonella* larvae were exposed to infective juveniles in sand for 2-5 days. At 9 ºC Hf85 was significantly superior to other isolates. Pathogenicity of *S. carpocapsae* was significantly higher at lower temperatures (5-25 ºC) than at the highest temperature (35 ºC). Conversely, pathogenicity of *S. glaseri* was significantly higher at high temperatures (15-35 ºC) than at lowest temperature of 5 ºC [27, 28] Stated that low temperatures significantly reduced the emergence of *H. bacteriophora* and significantly delayed the emergence of *S. carpocapsae* and *S. glaseri* but had no effect on the rate of emergence of *S. feltiae*. At 25 ºC and 75 per cent relative humidity (RH), all infective juveniles had died at the cadaver by day 28. At 15 ºC, 28 per cent of infective juveniles survived in the cadaver after 40 days but could only emerge after the cadavers were immersed in water for 24h. [29] observed that a nematode strain EAS 59 of *H. indica* isolated from southern Egypt was tested for single and combined effects of soil temperature exposed time and host (*S. littoralis*) introduction. Nematode incubation at 35 ºC for only 5 h before host introduction at 23ºC stimulated more nematode reproduction than at any other incubation periods. *H. indica* (EAS 59) reported here in possesses better persistence at high temperature, in terms of reproduction efficiency than other Entomopathogeinc nematode species. [30] Reported that *S. glaseri* was not able to survive on *G. mellonella* at above 35 ºC. The nematode developed and reproduced at 15-30 ºC and progeny production was greatest at 28 ºC. [31] Reported that the infectivity of five *Heterorhabditid* nematodes to *C. cephalonica* was much better at 25 ºC than at 35 ºC. [32] Reported that the pathogenicity of *Heterorhabditis* sp. was significantly different at temperatures of 20 ºC, 24 ºC and 30 ºC and the most conducive temperature was 24 ºC. [33] Studied the effect of heat-shock treatment and viability of some isolates of *Steinernema* spp. and *Heterorhabditis* spp. at relatively high temperatures. Nematode survival, infectivity and multiplication were unaffected at sub lethal temperatures of 35 ºC and 37 ºC. Exposure to 40ºC affected the survival and infectivity of both *Steinernema* spp. and *Heterorhabditis* spp. Host mortality, penetration of infective juveniles, time taken for infective juvenile emergence and multiplication of *H. indica* and *S. glaseri* at 20 ºC, 25 ºC, 30 ºC and 35 ºC were studied. The results revealed that both the nematodes caused mortality of *C. cephalonica* at all the above temperatures tested. The optimum temperature for highest mortality of *C. cephalonica* was 30 ºC and 35 ºC for *H. indica* and 25 ºC for *S. glaseri.* The highest number of infective juveniles emerged for both the nematodes after the completion of life cycle inside the host was at 30 ºC [34, 35] studied the effects of temperature and RH on the emergence and production of infective juveniles of *H. indica*. Larvae of *G. mellonella* were infected with 100 IJ/larva of *H. indica* at 25ºC and 100 per cent RH. The cadavers were exposed to varying degrees of temperature *viz*., 15ºC, 20ºC, 25ºC and 30ºC. The earliest emergence of infective juveniles occurred at 25ºC (8 days). [36] Studied the influence of temperature on *S. thermophilum.* The highest mortality, higher number of infective juvenile emergence and the time taken for infective juvenile emergence was lesser on *C. cephalonica* when observed at 30 ºC and 35 ºC. Highest number of infective juvenile's penetration was observed at 30 ºC. [37] investigated the effects of temperature ranged from 13 ºC, 18 ºC, 24 ºC, 30 ºC or 35 ºC on the virulence, development, reproduction and mortality of two Korean isolates of *S. glaseri* Dongrae strain and *S. longicadum* Nonsan strain on *G. mellonella*. Both the nematode species caused mortality at all temperatures. Highest mortalities were observed at temperatures between 24 ºC and 30 ºC. *S. longicadum* was better adopted to cold temperature and caused higher mortality at 18ºC than *S. glaseri*. All the temperatures were found better for the development of both the nematodes but progeny production was not observed at 13 ºC and 15 ºC. The progeny production

was better at 24 ºC and 30 ºC for *S. glaseri* and *S. longicadum* respectively. The mortality was better at 24 ºC for *S. glaseri* and best for *S. longicadum* at 24 ºC and 30 ºC respectively. [38] Reported the effect of temperature on the life cycle of *S. abbasi* and *H. indica* which revealed that infective juveniles were able to penetrate *G. mellonella* at temperature range between 20 ºC and 30 ºC for both the species. The maximum number of infective juveniles of *S. abbasi* and *H. indica* emerged from *G. mellonella* larvae at 30 ºC and 25 ºC. [39] Studied the impact of soil temperature on the virulence of the entomopathogenic nematodes *S. carpocapsae* and *S. feltiae*. The effect of temperature of 10 ºC, 15 ºC, and 25 ºC tested against the larvae of *Tenebrio molitor*. The nematodes were tested at two concentrations of 50 nematodes and 500 nematodes per box. *S. carpocapsae* was generally significantly more efficient at the highest temperature (25 ºC) than *S. feltiae*, especially at the lower concentration of 50 nematodes per box. *S. feltiae* recorded higher insect mortality at lower temperatures (15 ºC and 10 ºC). [40] Reported that the lipid reserves were conserved for longer storage periods at 8 ºC, 16 ºC, and 20 ºC, while at 24 ºC and 28 ºC the percentage of lipids decreased rapidly. The infectivity of infective juveniles of *Heterorhabditis* spp. was less tolerant than those of *steinernema* spp. to temperature of 8 ºC, 16 ºC, and 20ºC. [41] Investigated the effect of low temperature on the activity of the entomopathogenic nematodes, *Heterorhabditis indica* and *Steinernema glaseri*. The effects of low temperature at 5ºC to 25ºC were tested under BOD conditions. The survival and infectivity of entomopathogenic nematodes in insect host were studied. Survival of *H. indica* was significantly greater at the lowest temperature of 100 ºC. Conversely survival of *S. glaseri* was significantly greater at a temperature of 5 ºC and 100 ºC. The infectivity of *H. indica* and *S. glaseri* was effective at temperature of 20 ºC and 25 ºC (100% and 100%, respectively) for *S. glaseri* 10 ºC, 15 ºC and 20 ºC (74.00%, 100% and 100% respectively).

2.2. Effect of moisture

Entomopathogenic nematodes have some undesirable attributes such as short survival under rapidly fluctuating moisture conditions, requirement of a high humidity for favourable activity. Soil moisture is also an important factor for nematode mobility and survival [42, 10], EPNs require adequate soil moisture for survival and movement, but too much moisture may cause oxygen deprivation and restrict movement [6]. EPN survival is poor once water has been lost from the substrate [43-45] revealed that *Heterorhabditis* low potential to survive desiccation. According to studies by [3, 46, 10] nematode viability is affected when suddenly exposed to dry soil, but if humidity is decreased progressively, the nematode can adapt and enter anhydrobiosis.

Among many factors affecting the nematode activity in soil, moisture is considered to be more important. Soil moisture levels varying between 10 and 30 per cent had no significant effect on nematode survival; however there was a significant interaction between the quadratic component of temperature and linear component of soil moisture [47, 48] Conducted studies on the influence of soil texture and soil moisture on the infectivity of *Heterorhabditis* sp. D1 and *S. glaseri* KG against larvae of the sheep blowfly, *Lucilia cuprina* indicated that parasitism was less in soils of high clay content with the larger nematode *S. glaseri*. Parasitism in loamy and sand occurred at low moisture potentials equivalent to or below the permanent wilting points of plants. In sand both the nematode species parasitized larvae at high moisture potentials close to saturation. [49] Reported that *S. glaseri* moved horizontally upto 40 cm in 48h, when the water content of soil was kept to 19 per cent. With the reduction of soil water content, nematode mobility was affected. Large number of infective juveniles emerged from cadavers of *G. mellonella* containing *S. carpocapsae*, *S. glaseri*or *H. bacteriophora* at >-5MPa. *S. riobrave* emerged only at >-0.3MPa. No infective juvenile emergence was observed from cadavers at -500MPa (very dry) [50, 51] conducted moisture studies for *H. bacteriophora* (Oswego strain and Tuscarora strain) and *S. glaseri* (NC1 strain) by applying on sandy loam soils ranging from the permanent wilting point of plants to near saturation. Nematode virulence was evaluated by measuring insect mortality in *G. mellonella* larvae bioassays. Insect mortality increased with soil moisture content for both *H. bacteriophora* isolates but was highest in relatively low moisture soils (approximately -15bar) for *S. glaseri.* Insect mortality was generally lesser in low moisture soil before rehydration but rebounded to high levels on post hydration. [52] Studied the influence of moisture on host mortality, penetration, duration for emergence and number of infective juveniles emerged of entomopathogenic nematodes (*H. indica* and *S. glaseri*) from the host *C. cephalonica*. Maximum mortality of 100 per cent was observed under 100 per cent moisture level for *H. indica* and 70 per cent moisture level for *S. glaseri.* The highest number of infective juveniles of *H. indica* (18.10 IJ/ larva) and *S. glaseri* (11.01 IJ/larva) penetrated at 100 and 70 per cent moisture levels respectively. The earliest emergence of infective juveniles was observed at 6.8 and 4.2 days for *H. indica* and *S. glaseri* at the moisture levels of 100 and 70 to 90 per cent respectively. [53] Studied the influence of moisture on *S. thermophilum* against *C. cephalonica* larvae. The host mortality, penetration, time taken for infective juveniles emergence and number of infective juveniles emerged on the host *C. cephalonica* with 100 per cent mortality was reported at 100 per cent moisture level followed by 90 per cent respectively. Highest number of infective juvenile penetration and least time taken for the emergence of infective juveniles was observed at 100 per cent moisture level. The highest number of infective juveniles emerged from *C. cephalonica* at 100 per cent moisture level respectively. [54] Studied the efficacy of *S. carpocapsae* and *H. indica* against *S. litura* at different soil moisture levels. The median lethal concentrations of H. *indica* (10.8, 13.8, 23.8 and 15.7 IJ/larva) were lower than *S. carpocapsae* (13.8, 15.9, 28.8 and 19.4 IJ/larva) in sand, red and black soils at 10 per cent moisture level and at 15 per cent moisture level in black soil, respectively after 48h of post infection in third instar larvae of *S. litura*. The pathogenic effects of nematodes were better in sandy soil followed by red soil at 10 per cent moisture level and black soil at 15 and 10 per cent moisture levels. [3] Conducted studies on the effect of soil moisture on *H. bacteriophora*, *H. zealandica*, *S. scarabaei* and *S. glaseri* against white grubs on sandy loam and for *S. scarabaei* with loamy sand and silt loam soils. Infectivity test was conducted with third-instar larvae of Japanese beetle, *Popillia japonica* under laboratory condition. Nematode infectivity was highest at moderate soil moisture level (-10 to -100kPa) and lower in wet (-1kPa) and moderately dry (-1000kPa). Persistence was short at -10kPa, slightly improved at -100kPa, significant at -1000kPa and was highest at -3000kPa. Both *Steinernema* spp. persistence was very well at -10kPa. [10] Studied the influence of soil moisture on the infectivity of *Heterorhabditis* sp. and

S. carpocapsae at three level of relative soil moisture (100, 75, and 50% of field capacity). The maximum mortality of 86.7 and 80.00 per cent for *S. carpocapsae* and *Heterorhabditis* sp. respectively observed at 31ºC. At 25ºC, the highest mortality for both species was obtained at 75 per cent of field capacity (96.7% and 26.7%) for *S. carpocapsae* and *Heterorhabditis* sp., respectively. [55] Revealed that the soil moisture has marked influence on establishment of infective juveniles of different nematodes species in insect host. The establishment of *S. thermophilum* was noticed at soil moisture of 4 per cent and above whereas *H. indica* and *S. glaseri* established well at a soil moisture level of 5 per cent and above. The optimums soil moisture for *H. indica* (8-18%), *S. thermophilum* (6-20%) and *S. glaseri* (8-25%) for their establishment have been documented. A soil moisture of 6 per cent in soil is essentially needed for achieving 100 per cent host mortality for all the above three nematode species. [56] Reported that Entomopathogenic nematodes are not effective at high temperature; sensitive to ultraviolet light and require adequate moisture and high relative humidity for survival for reasonable length of time. The soil moisture effects on the activity of entomopathogenic nematodes *viz*., *H. indica* and *S. glaseri*. The levels of soil moisture at 3 to 25% were tested under laboratory conditions. The survival and infectivity of entomopathogenic nematodes in insect host were studied. The survival of *H. indica* and *S. glaseri* was observed at 4 and 5% soil moisture respectively. The last instar larvae of *Corcyra cephalonica* showed 100% mortality at 14 to 25% soil moisture for *H. indica* and 16 to 25% soil moisture for *S. glaseri*.

2.3. Effect of ultra violet radiation

Ultra violet (UV) rays from sunlight affect entomopathogenic nematodes adversely. [57] Reported that infective juveniles of *S. carpocapsae* were actually sensitive to short UV radiation (254 nm) at natural sunlight. High, but delayed nematode mortality was accompanied with UV exposure. Irradiation rapidly reduced nematode pathogenicity and nematodes exposed for seven minutes were unable to cause lethal infections in *G. mellonella* larvae. The median survival time of *G. mellonella* larvae increased progressively as nematode exposure to UV was lengthened. Inhibition of nematode reproduction and development was noticed at an exposure period longer than 2.45 and 5 min respectively. Direct exposure to sunlight also reduced pathogenicity at a range of 6.9 to 94.9 per cent at 30 and 60 min of exposure respectively. Long UV (366 nm) did not affect juveniles at any period of exposure. [58] Reported that *S. carpocapsae* exposed to UV radiation (240 nm) for 7 min were unable to cause lethal infections in *G. mellonella* larvae. Reproduction and development were inhibited after exposure to UV for 2.45 and 5 min respectively, but mortality of juveniles was not affected. Exposure to direct sunlight, amino benzoic acid and ionizing gamma radiation (3 X 10^5rads) affected the pathogenicity of *S. carpocapsae*. [59] reported that environmental factors such as temperature above 30ºC, relative humidities below 90 per cent, wind and UV light were the major reasons for the discouraging results of nematodes against foliar insects. [60] Reported that entomopathogenic nematodes were sensitive to UV light and their survival on foliage as decreased by exposure to sunlight. Hence, UV protectants are added to the nematode formulation before application to foliage. [61] Studied the effect of UV radiation (254 nm) on the native isolates of *H. indica* and *Steinernema* sp. from Kerala, compared with an exotic species, *S. glaseri*. Absolute mortality of all three species was observed with continuous exposure to UV raditation for 120-135 nm. [62] Studied the effect of some optical brightners (OBs) and PABA as UV protectants for entomopathogenic nematodes under laboratory conditions. Infective juveniles of indigenous isolates of *Steinernema* sp. (SSLZ), PDBCEN 13.21, PDBCEN 14.1 and *H. indica* (PDBCEN 13.22 and PDBCEN 14.3) were subjected to irradiation in aqueous suspension of OBs and PABA. The results indicated the protective effect of optical brightners and PABA in reversing the deleterious effect of UV radiation on the nematodes. [63] Studied the effect of UV radiation on infective juveniles of *H. indica* and *S. glaseri*. The results revealed that UV light emitted from UV lamp of 15W caused 100 per cent mortality of *H. indica*and *S. glaseri* after 120 and 210 min of continuous exposure respectively. [64] Studied the effect of UV radiation on the infective juveniles of *S. thermophilum*. The results revealed that the UV radiation from a UV lamp of 15W caused 100 per cent mortality within 240 minutes of continuous exposure. These irradiated nematodes were failed to infect *C. cephalonica*. [65] Studied the effect of UV radiation on the survival of *S. apuliae.* Exposure of the nematode to the median-wave length of UV-C caused rapid mortality of the nematodes. [55] Revealed that Ultraviolet light emittedfrom a UV lamp of 15W caused 100 per cent mortalityof *H. indica* and *S. glaseri* after 120 and 210 minutes, respectively indicating both are sensitive to UV light. The infective juveniles exposed to UV light were failed to infect *C. cephalonica*.

2.4. Soil pH

Soil pH in most agro ecosystems, having a range of 4-8, is not likely to have any significant effect on EPNs, but a pH of 10 or higher is likely to be detrimental [66]. Soil pH in most agro ecosystem, having a range of 4-8, is not likely to have any significant effect on EPNs, but a pH of 10 or higher is likely to be detrimental [66]. In this study, the pH range of the soils was 4.5-5.7 which was well within the range that is considered tolerable by the EPNs. [67] Studied the effect of pH on the survival of indigenous isolates of *S. carpocapsae* strain PDBCEN 11 and *H. indica* strain PDBC EN 13.3. The survival of infective juveniles was tested at pH 5.0 levels varying from 2.0-9.0. Maximum survival of *H. indica* and *S. carpocapsae* was noticed at pH levels of 5.0 and 7.0 and least survival for the species were at pH least of 2.0 and 3.0. [68] Reported that infective juveniles of *H. indica* and *S. glaseri* recorded highest infectivity of 96.67% and 83.33% in acidic of pH 4.0 and 5.0. Both the strain showed lowest infectivity of 46.67% and 36.67% in alkaline pH of 9.9 and 10.0. The maximum frequently of the entomopathogenic nematodes were noticed at pH 5.3 to 6.3. The highest frequency of *Steinernema* sp. was with pH 5.0-6.0 and *Heterorhabdits* sp. 6.0 [69] (Shelmith *et al*., 2008). The percentage survival of *S. karii* was 24 and 20% at pH 4 and pH 6.4 respectively and that of *H. indica* was 23% at ph 6.4 and 6-11% at other levels of pH. *S. karii* and *S. virgalemense* caused higher mortality of banana pseudo stem weevil at pH of 4.0-5.4 than that pH 6.4 [70] (Shelmith 2009). [71] Revealed that Nematodes were found in soils of varying pH levels, although individual species preferred a certain degree of acidity. *S. bicornutum* and *H. megidis* were found only in alkaline soils, while others, such as *S. silvaticum*, only in acidic environments (pH<4.5).

2.5. Soil Texture

Soil texture affects nematode movement and survival [6]. Generally, compared with lighter soils, soils with higher clay content restrict nematode movement and have potential for reduced aeration, which can result in reduced nematode survival and efficacy. Survival decline most rapidly in clay soil followed by clay loam and sand or sandy loam [72]. Frequency of occurrence of EPNs was moderate in forest soil. This may be due to the fact that the forest soil had a high proportion of clay, which is prone to poor aeration and high water retention, a situation that limits their chances of survival. [73] Shown that soil texture affects nematode movement and survival. Other researchers have reported that clay soils restrict nematode movement and are poorly aerated, which results in reduced nematode survival and efficacy when used as biocontrol agents [74]. The effect of clay content on the population of EPNs was recorded whereby survival and efficacy of the EPNs increased in clay soils [75, 76] Examined four species of entomopathogenic nematodes *viz*., *S. carpocapsae*, *H. indica*, S. *abbasi* and *S. feltiae* which moved into the host and significantly caused maximum mortality in greater wax moth *G. mellonella* (L.) larvae 48h after inoculation at 10 cm depth. However, at 15 cm depth, they took 60 h to cause maximum mortality in both presence/absence of *M. incognita*. The per cent mortality of *G. mellonella* was found to be more when EPN were applied in the presence of *M. incognita* compared to the absence of the same. [70] reported that nematodes were found to prefer sandy loam soils; however, the highest species diversity was found in sandy soils. Some species of nematodes were associated with a specific type of soil. For example, *Steinernema silvaticum* and *Heterorhabditis bacteriophora* were found only in sands, and *H. megidis* predominantly in clay.

3. Agricultural Practices

Regular cultivation in the vegetable garden exposes nematodes to desiccation and lethal radiations of the sun. In addition, organic amendments, chemical fertilizers and pesticides are commonly used in vegetable production and these may have had detrimental effects on EPNs. Various agricultural land use systems are characterized by a varying degree in the use of farm inputs. When applied at recommended rates, most fertilizers have little impact on EPN efficacy [77] (Shapiro *et al*., 1996). However, fresh manure or high rates of chemical fertilizers (e.g., urea) can have detrimental effects to EPNs survival and efficacy [78] (Mannion *et al*., 2000). Lack of physical disturbance and favourable soil conditions, as characterized by stable land use systems, favours the success of control attempts using EPNs [69]. Under a conventional tillage regime, the soil surface tends to have greater fluctuations in temperature and moisture than under no-tillage or reduced tillage management and EPNs are often more frequently detected in reduced tillage regimes [68]. Occurrence of EPNs was lowest in the intensively cultivated vegetable garden compared to the pasture, coffee and planted forest agro ecosystems. EPNs might be less adapted to highly disturbed soils characterized by frequent tillage, high agrochemical input use and frequent fluctuations in environmental conditions. [79] Shapiro *et al*. (1999) have reported that fresh manure or high rates of chemical fertilizers such as urea can be detrimental to survival and efficacy of EPN. Several studies have been conducted on the effects of agrochemicals including acaricides, fungicides, herbicides and insecticides on different species of entomopathogenic nematodes. While some chemical pesticides such as dodine, methomyl and parathion have proven to be toxic to EPNs.

4. Conclusion

This review has shown that disturbance of soil in terms of abiotic factors have an influence on the activity of entomopathogenic nematodes. We conclude that information on environmental suitability of EPN should be useful to pest managers in order to predict the likelihood of establishment of exotic entomopathogenic nematodes where they are used in inundative biological control programs.

5. References

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