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Movement and infectivity of entomopathogenic nematodes in sandy loam soil from a carrot field in Nova Scotia: a laboratory study

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ABSTRACT

Entomopathogenic nematodes (EPNs) from the Heterorhabditidae and Steinernematidae families are predators of various insect species across multiple Orders. Use of EPNs as a pest management strategy has been of interest since the 1930s. Under field conditions, EPN's are challenging to use due to low viability in soils with variable and often low soil moisture levels, particularly in areas where irrigation is not a common practice. Four EPN products from BioBest (B-Green System (*Heterorhabditis bacteriophora*), Steiner System (*Steinernema feltiae*), Kraussei System (*Steinernema kraussei*) and Carpo System (*Steinernema carpocapsae*)) were evaluated for efficacy to infest *Galleria mellonella* larvae buried at three depths in sandy loam soil and adjusted to four soil moisture levels. B-Green and Carpo showed the greatest sensitivity to soil moisture with < 50% infectivity when soil moisture levels were < 10%. Kraussei and Steiner had > 60% infectivity at soil moisture levels of 6 and 8% and > 80% infectivity in soils with 10 or 15% moisture. B-Green and Carpo showed low infectivity when *Galleria mellonella* was buried at 5 or 7 cm, while Kraussei and Steiner had ≥ 60% infectivity at these depths. EPNs showing ability to infect *Galleria mellonella* across a range of depths and soil moisture levels would be most promising as candidates for pest management under field conditions with moderate rainfall during the summer months.

INTRODUCTION

Entomopathogenic nematodes (EPNs) are obligate predators on insect species across a wide range of Orders (Labaude and Griffin 2018). Naturally occurring in diverse ecosystems, members of the Heterorhabditidae and Steinernematidae families (Stock et al. 1999; Hominck 2002) have been of interest for insect control since the 1930s (Glaser and Farrell 1935, Girth et al. 1940). Numerous EPN products are now available and sold commercially to control a range of Dipteran, Coleopteran, Hymenopteran and Lepidopteran pests. Under field conditions, EPNs are often found to have variable efficacy and this has been attributed to soil moisture (Lewis and Raun 1978, Kain et al. 1981, Kaya 1990) with soil moisture identified as key for EPN survival, persistence and efficacy (Gauger et al. 1994, Koppenhöfer et al. 1997, Hazir et al. 2003). To address this challenge, application of EPNs with supplemental wetting or irrigation (Unnruh and Lacey 2001) or culture of native nematodes able to tolerate the local soil moisture conditions (Kumar et al. 2003) have been explored.

In Canada, regions where irrigation is not typically required due to natural rainfall, e.g. Nova Scotia or Prince Edward Island, use of EPNs could be a viable option. Naturally occurring EPNs are found throughout eastern Canada (Bélair et al. 2013) and include the species now commercially available within the *Steinernema* and *Heterorhabditis* genera. Across the globe, nematodes isolated from each geographic region are specific to the soil and climatic conditions of that area (Ansari et al. 2007, Redmond and Potter 2010). Mass culture of these isolates would provide an EPN specific to the climatic conditions of the region, however, mass culture is not always practical and isolation of the species not always possible. In Nova Scotia, EPNs are of interest to control carrot pests such as carrot weevil (*Listronotus oregonensis* LeConte (Coleoptera: Curculionidae)) and carrot rust fly (*Psila rosae* (Fabricius) (Diptera: Psilidae)). Both of these

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pests spend their pupal stage in the soil (Martel et al. 1976, Stevenson and Barszcz 1991) and adult carrot weevil move freely over the surface of the soil. Their exposure to EPNs would occur primarily during the pupal stage as pupae are typically found within the top 5 cm of soil. Adults on the surface would be exposed to EPNs upon application of the products and adult carrot weevil have been shown to burrow into the top few centimeters of soil (Bykova and Blatt 2018). Obtaining large numbers of either of these pests is challenging due to these species being difficult to rear in the laboratory. As such, a more readily available alternate prey, *Galleria mellonella* L. (Lepidoptera: Pyralidae) could be used as bait to provide information to evaluate these EPNs under laboratory conditions. Using sandy loam soil collected from a carrot field located in Nova Scotia, our objective was to evaluate four commercially available EPN products for ability to locate and infect a *Galleria mellonella* larvae buried at 3 depths (3, 5 and 7 cm) where these pest species are likely to be found at four (6, 8, 10 and 15%) moisture levels. These moisture levels were chosen as they represent the soil moisture range recorded from these soils during the growing season in Nova Scotia.

MATERIALS AND METHODS

EPN infectivity

Test arena

Cardboard tubes (5 cm diam. x 10 cm length) were used as a support for single-use wax paper liners. Liners were created using a piece of wax paper (Reynold's Cut-Rite Wax Paper) measuring approximately 12 x 8 cm. The rectangle was folded and taped to create a tube just under 5 cm diam. and 11 cm length. Sandy loam soil (60% sand, 30% silt and 10% clay) from a field (45.067984, -64.481709) was autoclaved in batches (max. 1.5 cm depth) for 30 min at 121°C, allowed to cool for 24 h, stirred and re-autoclaved before use. Soil moisture was adjusted using tap water and measured using a Field Scout TDR 100 probe (Spectrum Technologies, Aurora, Illinois, USA). At the start of a trial, each tube had soil to a depth of 2 cm added. A single host (see Host) was added and then buried with more soil to specific depths (see Treatments). EPN products were applied (see EPNs) and tubes folded to conserve moisture. After 48 h tubes were taken apart and *Galleria mellonella* larvae dissected to confirm EPN presence. *Galleria mellonella* larvae infected with EPNs were often dark brown to black in color and very soft to the touch after 48 hours. Control larvae after the same time period were still white and firm. Larvae with EPNs were counted and a percentage within each replicate (number infected / 10) was recorded. Experiments were conducted on a laboratory bench at ambient temperature (~20-22°C) and RH (~50-55%), with natural daylight during the months of March – July 2019. Daylength during this time period ranges from 12 – 14 hours per day. Given the experiments are occurring in a wrapped tube and the host is buried, it is not anticipated that daylength would impact the results of our experiments in any way.

Host

Galleria mellonella larvae (East Coast Exotics; Souris, Prince Edward Island) were used for these studies. Each cardboard tube (see Test Arena) contained 1 larvae. Ten individual larvae were used for each treatment and each treatment replicated 5 times. Prior to introduction into the tubes, larvae were frozen for 10 min at -20°C to reduce their ability to escape from the tubes during the experiments.

Treatments

Galleria mellonella larvae were buried at 3 depths: 3, 5 and 7 cm into sandy loam soil adjusted to 4 soil moisture levels: 6, 8, 10 and 15%. All combinations of depth x moisture (n=12 treatments) were used for all 4 products plus a control and replicated 5 times (n=60 within each product or control or 600 larvae for each product (10 larvae/replicate)).

EPNs

Four commercially available EPN products from BioBest (Halifax Seed, Halifax, Nova Scotia) were used for these studies. Steiner System: *Steinernema feltiae* (Stanuszek), Carpo System: *Steinernema carpocapsae* (Weiser), Kraussei System: *Steinernema kraussei* (Steiner) and B-Green System: *Heterorhabditis bacteriophora* Poinar. All products were mixed in tap water and applied within the hour at a rate of 1 million/m^2 infective juveniles, delivered by pipette in a 2 mL aliquot of water. Prior to application of the nematodes, a droplet of the nematode solution was observed under the microscope to ensure EPNs were alive and active. A set of controls for each treatment was included to ensure the autoclaving was successful in removing any naturally occurring nematodes. Controls were set up the same as the treatments and had 2 mL of tap water applied to them.

Statistics

Mean percentage of infested *Galleria mellonella* larvae within a treatment was transformed using $\sin^{-1}(x+0.5)$ compared across product, soil depth and soil moisture using an ANOVA in R (R Core Team 2016). All controls

had zero infectivity and were not included in the analysis.

RESULTS

EPN products showed significant and variable infectivity across soil depths and moisture levels (Table 1). Kraussei and Steiner Systems performed the best in the studies (Fig. 1), showing significantly greater infectivity than B-Green and Carpo Systems ($P < 0.001$). B-Green System (*Heterorhabditis bacteriophora*, Fig. 1A) showed significant differences across soil moisture levels ($P < 0.0001$) and depths ($P = 0.001$) (Table 2). Infectivity was poor (< 10%) when soil moisture levels were low (6 or 8%) and larvae buried at depths of 5 or 7 cm. Greater soil moisture (15%) was required for infectivity to reach > 80% and only when larvae were buried at a depth of 5 cm. Infectivity dropped to < 60% when buried at 7 cm at the 15% soil moisture level. Similarly, Carpo System (*Steinernema carpocapsae*, Fig. 1B) was also significant across soil moisture levels ($P < 0.0001$) and depths ($P < 0.0001$) (Table 2). Contrary to B-Green, Carpo System showed poor infectivity at high soil moisture levels. Best results (> 50% infectivity) were obtained when larvae were buried at 3 cm and soil moisture level was 6 or 8%.

Kraussei System (*Steinernema kraussei*, Fig. 1C) and Steiner System (*Steinernema feltiae*, Fig. 1D) showed the best infectivity across soil moisture levels. Both showed significant differences across soil moisture levels ($P = 0.003$ and 0.01, Kraussei and Steiner, respectively), but not depth ($P = 0.44$ and 0.99, Kraussei and Steiner, respectively, Table 2). Steiner System had > 80% of larvae infected when soil moisture was 6% and larvae buried at depths of 5 and 7 cm. At higher soil moisture levels (10 and 15%), Steiner System had > 80% infectivity only at the 3 cm depth. Infectivity dropped to < 70% when larvae were buried at the 5 and 7 cm depths at higher soil moisture levels (Fig. 1D). Kraussei System showed similar results in that the 6% soil moisture level had > 80% infectivity when larvae were buried at depths of 5 or 7 cm (Fig. 1C).

DISCUSSION

The ability of EPNs to locate hosts is critical for their success as a biocontrol agent. Carrot pest species spending part of their life in the soil tend to be present within the top 10 cm of the soil layer and nematodes, applied to the surface, need to be able to penetrate this upper soil layer to locate their hosts. Although increased soil moisture was expected to result in greater mobility of nematodes, this was not observed for all species. Individual foraging behavior of the nematode species may serve to explain these results. *Steinernema carpocapsae* (Carpo System) is classified as a sit-and-wait or ambush forager while *Heterorhabditis bacteriophora* (B-Green) is a cruise forager (Campbell and Lewis 2002, Lewis 2002). An ambush forager is described as being less mobile, waiting for their

Table 1: ANOVA table showing significance of soil depth and soil moisture on entomopathogenic nematode (EPN) ability to locate and infest *Galleria mellonella* larvae in sandy loam soil.

Variable	F_{df}, P
Entomopathogenic nematode (EPN) product	$112.65_{3,197}$, < 0.0001
Soil depth	$3.75_{2,197}$, 0.02
Soil moisture	$4.39_{3,197}$, 0.005
EPN product X soil depth	$2.16_{6,197}$, 0.04
EPN product X soil moisture	$6.48_{9,197}$, < 0.0001
Soil depth x soil moisture	$0.83_{6,197}$, 0.54
EPN product x soil depth x soil moisture	$3.82_{18,197}$, < 0.0001

Figure 1. Mean percentage (± SE) of *Galleria mellonella* larvae infected by four species of entomopathogenic nematodes buried at 3 depths in sandy loam soil at 4 moisture levels.

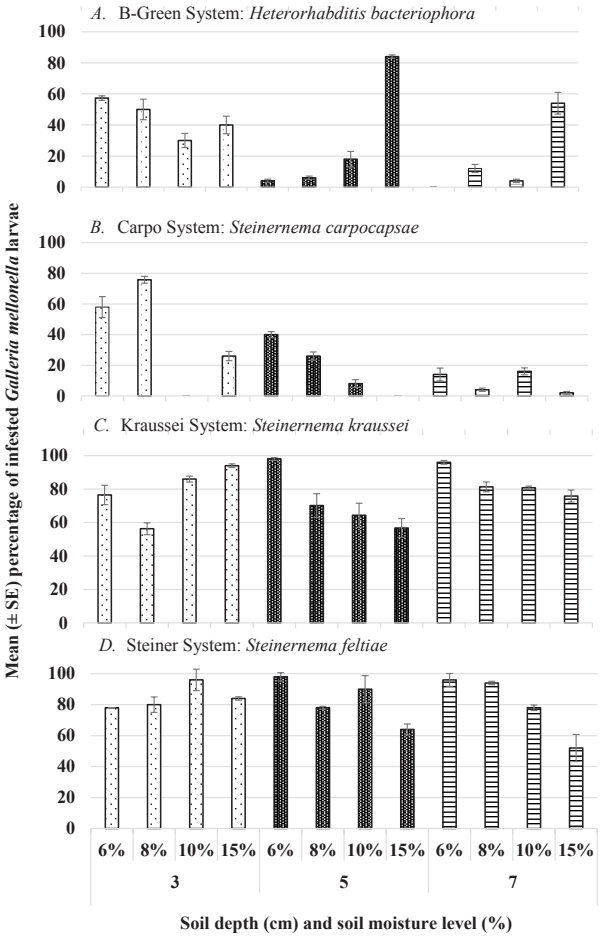

Table 2: ANOVA table showing significance of soil depth and soil moisture on entomopathogenic nematode (EPN) infectivity on *Galleria mellonella* larvae by commercial EPN product.

EPN Product*	Variable	F_{df}, P
B-Green	Moisture	$16.24_{3,50}$, < 0.0001
	Depth	$7.08_{2,50}$, 0.002
	Moisture*Depth	$6.35_{6,50}$, < 0.0001
Carpo System	Moisture	$18.31_{3,49}$, < 0.0001
	Depth	$25.08_{2,49}$, < 0.0001
	Moisture*Depth	$8.72_{6,49}$, < 0.0001
Kraussei System	Moisture	$3.23_{3,50}$, 0.03
	Depth	$0.46_{2,50}$, 0.63
	Moisture*Depth	$3.84_{6,50}$, 0.003
Steiner System	Moisture	$3.43_{3,48}$, 0.02
	Depth	$0.09_{2,48}$, 0.91
	Moisture*Depth	$1.00_{6,48}$, 0.43

* B-Green = *Heterorhabditis bacteriophora*, Carpo System = *Steinernema carpocapsae*, Kraussei System = *Steinernema kraussei*, Steiner System = *Steinernema feltiae*

prey to come close with the nematodes remaining near the soil surface (Hazir et al. 2003 and references therein). *Steinernema carpocapsae,* in a study from California, was found to stay in the upper 5 cm of soil, even when soil moisture was 13% (Koppenhöfer et al. 1995), consistent with results from our study. Bal and Grewal (2015) observed *Steinernema carpocapsae* to be highly mobile, migrating up to 11 cm, laterally, in search of a host and Lortkipanidze et al. (2016) observed high infectivity when hosts were placed on the surface. The role of substrate in these studies may also help explain these contradictory observations. Kruitbos et al. (2009) found *Steinernema carpocapsae* to infect hosts buried at depths of 35 cm when the substrate was peat, but limited infectivity at 15 cm when the substrate was sand. Koppenhöfer et al. (1995) used a sandy loam soil (75% sand, 18% silt and 7% clay) at 13% soil moisture in their studies (similar to our study), while Bal and Grewal (2015) used a silt loam topsoil (61.8% silt, 26.2% clay, and 2.6% sand) from a corn field at 24% soil moisture and Lortkipanidze et al. (2016) used 100% sand at 15% moisture. Carrot fields in Nova Scotia are a sandy loam comprised of approximately 60% sand, 30% silt and 10% clay. Molyneux and Redding (1984) found infectivity to be low in soils with high clay content and to occur in loamy sand at low moisture potentials below the permanent wilting point of plants. The lateral, instead of vertical, movement observed by Bal and Grewal (2015) could be the result of the high clay content in their substrate. Kaya (1990) studied the connection between nematode dispersal and soil porosity, showing that substrates with small pores experience low dispersal. Peat would have a greater soil porosity than sand and hence nematodes would be more widely dispersed in that substrate when compared with sand. In our study, the lack of infectivity by *Steinernema carpocapsae* at greater depths, even with high soil moisture content could be attributed to the soil composition and hence pore size of the substrate. Wilson et al. (2012) questioned whether *Steinernema carpocapsae* can be considered a strictly ambush forager as they observed both ambush and cruiser strategies under certain conditions.

Cruiser foraging behavior refers to nematodes which are highly mobile and distributed throughout the soil profile (Hazir et al. 2003). *Heterorhabditis bacteriophora* has been described as a cruise forager and was observed to locate and infect non-mobile hosts (*Galleria mellonella* held stationary in a wire mesh cage) better than mobile hosts when placed on the surface of the soil (Bal and Grewal 2015). Lortkipanidze et al. (2016) found *Heterorhabditis bacteriophora* to be more virulent when hosts were buried in a sand column, which is not consistent with our results, but the higher clay content of sandy loam may be sufficient to reduce movement. Kruitbos et al. (2009) observed another *Heterorhabditis* species, *Heterorhabditis megidis,* to locate hosts at depths of 45 cm when buried in sand, but no soil moisture level was noted in that study. As *Heterorhabditis bacteriophora* showed infectivity in hosts buried at 5 and 7 cm depths in soil of 15% moisture but not at lesser soil moisture levels, we suggest that soil moisture can serve to increase the range of mobility for species sensitive to substrate.

The other cruiser strategist in our study was *Steinernema kraussei* (Kraussei System). Described as a cruiser by Campbell et al. (2003), it has been studied for control of Pales weevil, *Hylobius abietis* (Torr et al. 2007). In sandy loam soil, under all soil moisture levels, *Steinernema kraussei* was able to infect hosts with > 50% success. Given *Heterorhabditis bacteriophora* and *Steinernema kraussei* use the cruiser foraging strategy, it would be expected that they would have similar infectivity results. Both species are of similar diameter (32 µm and 24 µm, *Steinernema kraussei* and *Heterorhabditis bacteriophora*, respectively), but not length (948.1 µm and 582.0 µm, *Steinernema kraussei* and *Heterorhabditis bacteriophora*, respectively) (Gokce et al. 2013, Kary 2010). It is possible that the longer length of *Steinernema kraussei* allows the nematode to move more readily within the soil pores of the sandy loam, while the shorter length of *Heterorhabditis bacteriophora* hinders such movement.

A third category of foraging behavior, 'intermediate', refers to nematodes which display some ambush

behavior but also capacity to disperse and seek their hosts. *Steinernema feltiae* (Steiner System) is considered an 'intermediate' forager (Campbell and Gaugler 1997). These strategists are described as adapted to infecting insects within the top 5 cm of the soil, including pupae of Diptera and Coleoptera. In our study, *Steinernema feltiae* was able to locate and infect > 50% of the hosts across all soil moisture levels and to depths of 7 cm. Campbell and Gaugler (1997) used a fine layer of sand which did not allow for vertical movement, hence it is likely that sandy loam is a substrate which allows the species to disperse.

Based on the results from our study, all four EPN products would have potential to control carrot pests such as carrot weevil and carrot rust fly. Both pest species would be in the soil as pupae and carrot weevil adults spend considerable time on the soil surface. Under field conditions, soil moisture levels can drop below 10%, and all four EPN products were able to infect hosts under these conditions in the laboratory setting. Field studies to confirm these observations and evaluate their potential against carrot pests are recommended.

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