



Effect of habitat and soil management on dispersal and distribution patterns of entomopathogenic nematodes



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ABSTRACT

Previous research has documented patchy distributions of entomopathogenic nematodes (EPNs) in the field, but more uniform distributions of EPNs could increase their biocontrol services in agroecosystems. Although laboratory studies have identified variation in foraging behavior of EPN species, less data is available on factors influencing their dispersal and resulting distribution patterns in the field. We examined the effect of biotic environmental factors including habitat type and plant cover, soil management and associated arthropod composition on the short- and long-term dispersal potential of *Steinernema carpocapsae* ALL and *Heterorhabditis bacteriophora* GPS11 emerging from nematode-infected host cadavers in the field. Based on bait trapping in the soil, both EPN species showed equivalent potential to disperse up to 2 m, actively or passively, in both grass and cultivated potatoes. Arthropod abundance, assessed by pitfall traps and soil core sampling, was equal in the two habitats. *S. carpocapsae* was detected in larger numbers in the water in pitfall traps, whereas *H. bacteriophora* numbers were positively correlated with mites in soil core samples. We documented aggregation of *H. bacteriophora* populations over the two years of the study in vegetable plots, which is consistent with earlier studies. Spatial distributions after dispersing from a grassy border into the adjacent cultivated field plots were more aggregated for *H. bacteriophora* than for *S. carpocapsae*. In most cases, no significant differences in the dispersal and spatial distribution of generally low population densities of *H. bacteriophora* were observed in plots with different soil management regimes, the exception being significantly lower aggregation in the first year of the study in plots with reduced tillage, cover crops, and no herbicide or insecticide treatments.

1. Introduction

Entomopathogenic nematodes (EPNs) are often applied as biological control agents with short-term effect (Grewal et al., 2005). However, their natural widespread occurrence in diverse ecosystems (Stock et al., 1999; Hominick, 2002) and persistence beyond a single season, in some managed ecosystems (e.g. Klein and Georgis, 1992; Alumai et al., 2006; Bal et al., 2014c), suggest that the preventive approach of conservation biological control may be feasible. An effective conservation approach requires knowledge of the dispersal behavior of EPNs and how distribution is affected by agricultural soil management. This knowledge is critical for the development of field application techniques that hope to expand the patchy distribution of EPN populations (Stuart and Gaugler, 1994; Glazer et al., 1996; Campbell et al., 1995, 1996, 1998; Wilson et al., 2003; Stuart et al., 2006; Spiridonov et al., 2007) to a more

uniform distribution designed to increase the percentage of target insect pests contacted and infected.

Laboratory studies have identified variation in foraging and host finding behavior of EPN species in controlled environments. The third stage infective juvenile (IJ) is the only free living stage in the life cycle of the EPNs that searches for host insects in or on soil. EPN species have been classified as cruisers (actively searching), ambushers (more sedentary and waiting for hosts) and intermediate foragers based on their host finding tactics (Lewis et al., 1992; Campbell and Gaugler, 1993; Grewal et al., 1994). Cruisers, such as *Heterorhabditis bacteriophora*, are able to find below ground sedentary hosts (Alatorre-Rosas and Kaya, 1990; Grewal et al., 1994) using active search (Lewis et al., 1992; Campbell and Gaugler, 1993) and an ability to orient to volatiles that serve as host cues (Lewis et al., 1993; Grewal et al., 1994). Ambushers, such as *Steinernema carpocapsae*, are more effective at attaching to

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mobile hosts (Lewis et al., 1992; Campbell and Gaugler, 1993) with low motility (Lewis et al., 1992; Campbell and Gaugler, 1993) and nictation or tail standing (Campbell and Gaugler, 1993; Kruitbos and Wilson, 2010). The foraging behavior of EPNs is likely habitat specific (Wilson et al., 2012) and their dispersal is influenced by a number of factors including vegetation (Bal et al., 2014a), host presence (Hui and Webster, 2000; Cutler and Webster, 2003; Ali et al., 2012; Turlings et al., 2012; Bal and Grewal, 2015) and absence (Bird and Bird, 1986; Ishibashi and Kondo, 1990; Shapiro-Ilan et al., 2014; Bal et al., 2014a), as well as host suitability (Grewal et al., 1997). Recently, we discovered that in the absence of hosts, a small proportion of the population of the ambusher species, *S. carpocapsae* disperses long distances in a short period of time, resulting in the same average daily dispersal rate as the cruiser, *H. bacteriophora* (Bal et al., 2014a). This “sprinting” trait was amenable to genetic selection for increased proportion of sprinters although there were trade-offs that included reduced nictation ability and reproduction (Bal et al., 2014b).

Although the foraging behavior of EPN species has been well-studied under laboratory conditions, little is known about how these foraging strategies influence dispersal and distribution patterns of in-undatively applied EPNs in the field (Poinar and Hom, 1986; Campbell et al., 1998; Del Valle et al., 2008; Jabbour and Barbercheck, 2008). Further, there is little information on dispersal behavior of EPNs released via nematode infected host cadavers in the field (Del Valle et al., 2008; Jabbour and Barbercheck, 2008; Dolinski et al., 2015). Earlier studies have shown that a number of factors may influence EPN distributions in the field including: abiotic edaphic factors such as texture and moisture (Georgis and Poinar, 1983; Kung et al., 1991), biotic environmental factors such as plant habitat type (Campbell et al., 1998; Efron et al., 2001; Lawrence et al., 2006; Alumai et al., 2006), presence or absence of host and non-host invertebrates and their spatial distribution in the soil profile (Mráček, 1980, 1982; Campbell et al., 1995; Puza and Mráček, 2005), and the many combinations of these factors (Hoy et al., 2008). Factors such as invertebrate abundance, organic matter, and soil moisture retention can be influenced by soil management practices (Benton et al., 2003; Geiger et al., 2010; Jalota et al., 2006; Kovacs-Hostyanszki et al., 2013; Van Wie et al., 2013) such as reduced tillage and compost amendment (Nahar et al., 2006; Briar et al., 2007), which in turn serves to increase EPN abundance by increasing the nematode food web enrichment and structure indices, and leading to lower P, higher K, and lower C:N ratio (Hoy et al., 2008). In particular, the detection of endemic populations of EPNs have been reported to be more frequent in grassy areas than in neighboring cultivated fields (Alumai et al., 2006; Lawrence et al., 2006; Campos-Herrera et al., 2007). In addition, EPNs are known to disperse more actively in soils that are higher in organic matter (Kruitbos et al., 2010; MacMillan et al., 2009; Wilson et al., 2012) but their distribution within the soil is patchy, particularly in managed ecosystems, possibly associated with the patchy distribution of hosts (Campbell et al., 1998; Stuart et al., 2006).

The goals of this research were to measure and compare the short-term dispersal potential and distribution patterns of two EPN species with different foraging strategies, *H. bacteriophora* and *S. carpocapsae*, in response to plant habitat and cultural practices that influence plant habitat and its associated arthropod populations. Dispersal and distributions were directly compared in response to grass and cultivated potato. We then tested the effect of soil management including reduced tillage, cover crops (clover and barley), and a compost amendment on the long-term dispersal of *H. bacteriophora* from grassy borders to adjacent cultivated fields where pest control is desired. Given the potential influence of insects and microarthropods on phoretic dispersal and spatial distribution of EPNs (Kaya, 1990; Epsky et al., 1988; Timper et al., 1988; Parkman et al., 1993; Mráček and Bečvář, 2000; Kruitbos et al., 2009), we compared EPN dispersal from the two soil management regimes with and without insecticide applications in a factorial experiment.

Because the average displacement of the two EPN species in the absence of hosts in the laboratory is similar, we hypothesized similar dispersal rates for the two EPN species in the field. Because *S. carpocapsae* is effective in contacting mobile hosts due to its nictation ability, we hypothesized that the dispersal of the two EPN species would differ according to the abundance of arthropod communities in a given habitat. However, we hypothesized more uniform distribution of *S. carpocapsae* than *H. bacteriophora* because a small proportion of the *S. carpocapsae* population may disperse farther and faster than *H. bacteriophora* in the absence of host insects, as they do in the laboratory, and phoretic dispersal facilitated by nictation behavior may enhance their dispersal in the presence of insect hosts. Given the impact of soil management on EPN abundance and survival and greater EPN occurrence in grass than neighboring cultivated fields, the altered soil management was hypothesized to create conditions that increase both active and phoretic movement of *H. bacteriophora* from grassy borders into adjacent vegetable fields, leading to a more uniform spatial distribution of IJs in the cultivated areas, such that their biological control services would be more widely available.

2. Materials and methods

2.1. EPN infected cadaver production

Two nematode species, *Heterorhabditis bacteriophora* GPS11 (a cruiser) and *Steinernema carpocapsae* ALL (an ambusher) were obtained from our laboratory collection maintained at -196°C . New live cultures were raised for this study by infecting final instar wax moth larvae, *Galleria mellonella* (L.), obtained from Vanderhoest Canning Company, St. Mary's, Ohio (Kaya and Stock, 1997). EPN species were released using EPN-infected *G. mellonella* cadavers rather than aqueous suspensions, to mimic natural conditions and to maximize IJ dispersal, survival and infectivity (Shapiro and Glazer, 1996; Shapiro-Ilan and Lewis, 1999; Perez et al., 2003). Cadavers were prepared by exposing final instar *G. mellonella* to ca. 400 freshly produced infective juveniles (IJs) of *H. bacteriophora* or *S. carpocapsae* in $15\text{ cm} \times 2\text{ cm}$ Petri dishes. After 3 days at 22°C infected insects were transferred to White traps (Kaya and Stock, 1997) and monitored for initial emergence of IJs. Cadavers were applied to field plots within 24 h of initial IJ emergence, typically after 10 days (Bal et al., 2014a).

2.2. Short-term dispersal

2.2.1. Effect of habitat on short-term dispersal and distribution patterns of two EPN species in the soil

2.2.1.1. Plot establishment. The experiment was performed in grassy borders and neighboring cultivated potato field plots in Canfield silt loam soil (2–6% organic matter) at a farm in Shreve, OH (SC, Latitude: $40^{\circ}: 40' \text{ N}$, Longitude: $-83^{\circ}: 58' \text{ W}$). Short-term dispersal was studied in a split-plot experiment with EPN species (*H. bacteriophora* vs. *S. carpocapsae*) as the main factor and habitat (grassy border vs. potato field plots) nested within the main factor over a period of 96 h. The experiment was performed in an area 76 m long and 7 m wide containing a potato field and adjoining grassy border, both divided into four 15 m sections (Fig. 1). The experiment was set up in two $15\text{ m} \times 7\text{ m}$ main plots during the week of August 15th to 20th, 2011 (Replicate 1). *H. bacteriophora* dispersal was studied in one plot and *S. carpocapsae* dispersal in the other plot, 3.8 m apart, to avoid interspecific competition between the two EPN species. The experiment was repeated once in the other two $15\text{ m} \times 7\text{ m}$ main plots of the field strip for both *H. bacteriophora* and *S. carpocapsae* in the week of August 29th to September 3rd, 2011 (Replicate 2) keeping a buffer zone of $7.6\text{ m} \times 7\text{ m}$ between the two experimental field strips. Each $15\text{ m} \times 7\text{ m}$ section was divided into five $3\text{ m} \times 3\text{ m}$ plots for each EPN species in each habitat type. The land was managed without any chemical inputs and the potato field was covered with mulch during the

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