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Soil and habitat complexity effects on movement of the entomopathogenic nematode *Steinernema carpocapsae* in maize

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ABSTRACT

Habitat heterogeneity enhances conservation of aboveground biological control organisms in agricultural systems. Complex habitats may also conserve beneficial organisms in the soil, although this has rarely been examined in field experiments. We compared the effect of simple (maize) and more complex (maize plus mixed annual plant refuge) habitats on the persistence and dispersal of the entomopathogenic nematode *Steinernema carpocapsae* applied to soil as nematode-killed insects. The experiment was conducted twice, in 2005 and 2006. We quantified *S. carpocapsae* dispersal by bioassay of soil samples collected at distances up to 3 m away from the application point within and between crop and refuge habitats. We detected *S. carpocapsae* in 1.4% (2005) and 0% (2006) of control site samples. *S. carpocapsae* detection at the source was not affected by habitat complexity but was associated with soil bulk density, plant density, and soil matric potential. The maximum movement rate was 33.3 cm/day, 9 days after application, which exceeded previously reported rates of 7.5 cm/day. *S. carpocapsae* detection decreased with increasing distance away from the application point. In 2005, soil moisture affected dispersal such that *S. carpocapsae* were detected further away in complex habitats, when the soil moisture in this habitat was higher. In 2006, movement was similar in both habitats, likely due to similarities in overall plant density in both treatments that year. Our results indicate that movement of *S. carpocapsae* is not necessarily dependent on habitat complexity but may respond to variation in factors associated with overall plant density, and subsequently, soil moisture.

1. Introduction

Habitat complexity in agroecosystems can enhance ecosystem services such as biological control and pollination by conserving invertebrate diversity and promoting the survival and activity of beneficial organisms (Landis et al., 2000). Although this concept has been examined from the aboveground perspective (Landis et al., 2000; Thies and Tscharntke, 1999), relatively few studies have considered the effects of habitat complexity on soil-dwelling biological control organisms (but see Smith et al., 2008). Habitat complexity may affect soil biota positively or negatively via changes due to disturbance regimen (Hendrix et al., 1986; Millar and Barbercheck, 2002) and plant identity and diversity (De Deyn et al., 2004; St John et al., 2006).

We tested the effects of habitat complexity on the entomopathogenic nematode (EPN), *Steinernema carpocapsae* (Weiser). *S. carpocapsae* and other EPNs are obligate lethal parasites of soil-dwelling arthropods. We selected *S. carpocapsae* as a model because like other EPNs, it can impose considerable mortality in arthropod populations and has also been commercially exploited as a biological alternative to chemical control of soil-dwelling pests in agricultural systems (Grewal et al., 2005).

In agroecosystems, habitat complexity can be created through the planting of diverse strips of vegetation within or adjacent to crop areas that remain undisturbed during the field season. Such strips could serve as refuges that increase persistence by moderating abiotic factors critical to EPN survival such as soil moisture (Lawrence et al., 2006; Millar and Barbercheck, 2002) and temperature, or by increasing biotic diversity and enhancing the availability of host insects. Conversely, enhancing biotic diversity may lead to increased predation of EPNs (Baur et al., 1998; Epsky et al., 1988). Prior studies show EPN populations were detected more frequently in weedy and no-till maize than in less weedy and moldboard-plowed maize (Brust, 1991), as well as in grassy strips adjacent to crops than in clean cultivated crops (Lawrence et al., 2006). These results suggest a possible relationship between EPNs and habitat complexity as a function of disturbance and/or plant community.

The impact of refuge habitats on EPN persistence may be of little consequence if EPNs fail to move away from the refuge into the surrounding crop area to contribute to pest control. Even with recent interest in spatial soil ecology (Ettema and Wardle, 2002; Klironomos et al., 1999), dispersal is largely ignored in current field

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research addressing soil ecosystems (but see Van der Stoel and Van der Putten, 2006; Wilson et al., 2003). Infective juveniles (IJ), the only free-living stage of EPNs, disperse when they exit a nematode-killed insect and move through or across the soil to seek new hosts, a behavior critical for population persistence. We hypothesize complex habitats that provide favorable soil conditions will result in greater movement of EPNs than simple habitats that provide less favorable soil conditions. Considerable laboratory research has explored nematode movement in sand and soil, contributing information about movement in response to various abiotic and biotic cues, as well as effects of soil physical characteristics (reviewed in Downes and Griffin, 1996; Lewis et al., 2006), but few studies have explicitly examined short-term dispersal in the field (but see Hsiao and All, 1998; Poinar and Hom, 1986).

The goal of this experiment was to determine whether areas of diverse vegetation within a crop can contribute to the conservation of EPN populations. We examined the effects of habitat complexity on *S. carpocapsae* persistence and dispersal, as measured by detection over time after application within and between crop and refuge habitats.

2. Materials and methods

Research was conducted during two field seasons (2005, 2006) in different fields each year (0.6 ha) at the Russell E. Larson Agricultural Research Center in Rock Springs, Pennsylvania. The land was managed without chemical inputs during the experiment. Each field had a history of soybean (glyphosate-resistant *Glycine max* (L.) Merr., Dekalb DKB28-52 [2005] and Asgrow 2703 [2006]) cultivation in the previous year and was surrounded by a 10 m wide grassy border. A rye (*Secale cereale* L.) cover crop was fall-seeded in the year prior to the initiation of the experiment. Liquid dairy manure was applied to the entire field in early spring for fertility. Following cultivation of the rye, we planted untreated maize (*Zea mays* L., Pioneer 36B08) in 0.76 m rows at 69,000 plants/ha. We used in-row cultivation to control weeds in the maize once following planting, 9 and 14 days before *S. carpocapsae* application in 2005 and 2006, respectively.

We conducted a split-plot experiment with habitat complexity (complex vs. simple) as the main factor. The experiment consisted of 15 m × 15 m plots, of which only the inner 12.5 m × 12.5 m was sampled. Each habitat treatment was replicated six times, arranged in a randomized block design. The "simple" treatment consisted solely of the maize crop. To create habitat complexity, we planted a dicot–monocot seed blend (Beneficial Blend Seed Mix®, Rincon-Vitova, Ventura, CA) in a 0.75 m wide center row in the "complex" treatment, surrounded by the crop (Fig. 1). Following soybean harvest in November 2004, we broadcast the beneficial seed blend (15.7 kg/ha, 19 g/15 m × 0.75 m strip, mixed with sand) by hand into raked soil, and lightly raked the seed into the soil. For the 2005 experiment, we first seeded in November 2004, and two additional times in April 2005 to ensure refuge establishment. To ease maize planting and maintain row evenness, we planted maize into the refuge and then removed maize seedlings from the refuge by hand after germination. Due to poor establishment of the seed planted in November for the 2005 experiment, we planted the mix in April 2006. One seeding for the 2006 experiment was sufficient to achieve similar plant density in the refuge in both years.

Each main plot was split across the rows into two subplots: *S. carpocapsae* treatment and an untreated control. The center row of each *S. carpocapsae* treatment plot was designated as the application site. Maize was planted in the center row in the simple habitat, and the center row of the complex habitat consisted of the refuge strip. *S. carpocapsae* and control treatments were located at least 5 m away from one another. Immediately preceding nematode application, we assessed the abundance of naturally occurring EPNs in application and control treatments, and 1 m and 3 m away from the application site in four directions (within and across the crop rows). We used the standard bioassay technique (Kaya and Stock, 1997) described below to detect EPNs in treated and untreated experimental plots.

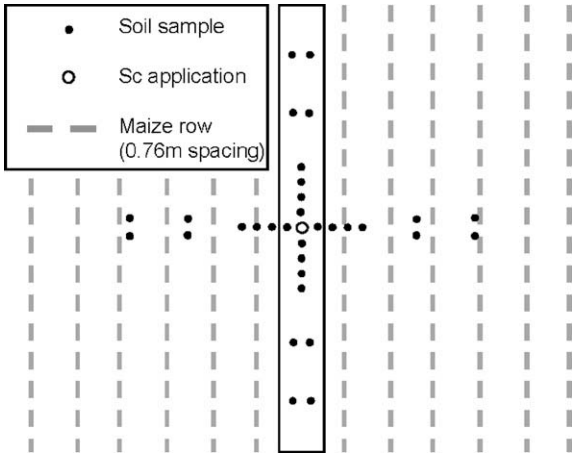

Fig. 1. Experimental plot design. Habitat complexity was manipulated by altering the center row area (0.76 m × 15 m, outlined above) of each experimental treatment replicate. In the center row of the "complex" habitat treatment plots, we planted an annual dicot–monocot seed blend (Beneficial Blend Seed Mix®, Rincon-Vitova). In the "simple" habitat treatment, the center row of each plot consisted of a maize row. The center row area in both habitat types was surrounded by maize. We applied *Steinernema carpocapsae* (Sc) to the center row in both experimental habitat types. Soil samples were collected at the application site, and at distances 0.25, 0.5, 0.75, 1, 2, and 3 m away within the center row and across rows. Control samples were collected from within the center row of each replicate, at least 5 m away from any EPN application point.

In the EPN treatment, we applied *S. carpocapsae* on July 6, 2005 and June 28, 2006 in the form of infected *Galleria mellonella* (L.) cadavers (Shapiro and Lewis, 1999) to mimic emergence from a naturally infected insect in a field setting. We selected *S. carpocapsae* because this species was isolated from another field at the Russell E. Larson Agricultural Research Center in 2004. Its identity was confirmed by Dr. Patricia Stock (University of Arizona). To obtain cadavers with nematodes, last-instar *G. mellonella* larvae were exposed to *S. carpocapsae* at the rate of 20 IJ/*G. mellonella*, 7 days before application in the field. The day before application, we placed two nematode-killed insects in each of two biopsy cassettes (Simport Plastics Histosette II, 0.5 × 2.75 × 4 cm with 0.1 cm^2 openings) and filled the cassette with moistened soil that had been pasteurized by microwave (Ferriss, 1984). Two cassettes were buried at the application site in each replicate and marked with survey tape so that the application site could be relocated.

To verify nematode emergence, one cassette from the application site in each replicate, along with 200 ml of surrounding soil in the top 15 cm, was removed 2 days after burial. A similar amount of soil was collected from each control treatment. The remaining cassette was removed 20 days (2005) or 12 days (2006) after burial, along with the surrounding soil, and another control site soil sample was collected. Subsequently, each soil sample collected to determine persistence and dispersal of *S. carpocapsae* consisted of two cores of 2.54 cm × 15.25 cm, a volume of 200 ml soil, from each sample point in each treatment and control replicate. After soil was collected from each sample point, the soil corer was wiped clean of all attached soil and rinsed with ethanol to prevent contamination between replicates. One soil corer was used exclusively for samples taken from control sites and cleaned between samples. Each sample was placed in a labeled plastic