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An analysis of using entomopathogenic nematodes against above-ground pests

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Abstract

Applications of entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae have traditionally been targeted against soil insects. Nonetheless, research over the last two decades highlights the potential of such agents against above-ground pests under certain circumstances. A general linear model was used to test for patterns in efficacy among 136 published trials with *Steinernema carpocapsae* Weiser, the most common species applied against foliar and other above-ground pests. The focus was on field and greenhouse assessments, rather than laboratory assays where relevant ecological barriers to infection are typically removed. The model showed differences in nematode treatment efficacy depending on the pests' target habitat (bore holes > cryptic foliage > exposed foliage) and trial location (greenhouse > field studies). Relative humidity and temperature during and up to 8 h post-application were also predicted to influence rates of nematode infection obtained. Conversely, spray adjuvants (both wetting agents and anti-desiccants) and nematode dosage applied (both concentration and use of consecutive applications 3–4 days apart) did not explain a significant amount of variance in nematode performance. With reference to case studies the model is used to discuss the relative importance of different factors on nematode efficacy and highlight priorities for workers considering using entomopathogenic nematodes to target pests in novel environments.

Introduction

Entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae and their symbiotic bacteria have generated significant interest as inundative biological control agents for use against insect pests (Klein, 1990; Poinar, 1990; Kaya & Gaugler, 1993; Liu *et al.*, 2000). Increased understanding of nematode biology, host range and epizootiology and concurrent advances in commercial production, storage and formulation, have led to nematode-based products being marketed worldwide over the last 20 years as safe alternatives to chemical insecticides (Friedman, 1990; Ehlers, 1996). To date, products based on *Steinernema* (= *Neoaplectana*) *carpocapsae* Weiser and *S. feltiae* (= *bibionis*) Bovien (Rhabditida: Steinernematidae) and *Heterorhabditis bacteriophora* (= *heliothidis*) Poinar (Rhabditida: Heterorhabditidae) are the most widely commercialized and have been almost entirely marketed as inundative applications for high value niche and specialty markets (Ehlers, 1996). Pests commonly controlled include fungus gnats (Sciaridae) in mushroom houses, cutworms and armyworms (Noctuidae) in vegetables and turfgrass, white grubs (Scarabaeidae) in vegetables and sugarcane and black vine weevil, *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae), in greenhouse and nursery stock (Klein, 1990; Georgis & Hague, 1991; Kaya & Gaugler, 1993; Ehlers, 1996). These examples encompass only soil- or root-dwelling pests, and the use of nematodes against above-ground pests

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remains negligible, despite a demand for effective microbial sprays against foliar pests (Cross *et al.*, 1999; Copping & Menn, 2000).

This dichotomy in target habitat use is best explained by the nematode's biology; the natural environment of entomopathogenic nematodes is the soil, where they are ubiquitous (Gaugler, 1988; Kaya, 1990; Hominick *et al.*, 1996) and foliar habitats provide conditions atypical for nematode activity and survival. Attempts to control foliage-feeding pests with nematodes from the mid 1950s to early 1980s were disappointing and commercial interest was likely discouraged by low host mortality or inability to adequately reduce foliage damage (Kaya, 1985; Begley, 1990). However, growing restrictions on the uses of chemical insecticides coupled with the increasing availability of nematode-based products during the intervening years has renewed interest in using nematodes in above-ground habitats. Entomopathogenic nematodes have now been tested in a range of habitats that include boreholes and galleries in stems or wood, leaf mines, curled leaves, reproductive structures (e.g. flowers, buds) as well as in the extreme case the leaf surface. Apart from the leaf surface, these habitats are cryptic, and thus may afford the infective juvenile stages some protection from unfavourable environmental conditions at the target site.

As with chemicals, optimal application strategies are needed to maximize the effectiveness of nematode sprays. Infective stage juveniles (IJ) may be applied to foliage using common agrochemical equipment, including hand-held pressurized sprayers, mist blowers, electrostatic or spinning disc systems and aircraft mounted atomizer sprayers (Georgis, 1990; Lello *et al.*, 1996). The infective juveniles can withstand the shear forces associated with delivery through a range of nozzle types with openings as small as 50 microns diameter and high hydraulic pressures (estimates range from 2–5 × 10^3 kPa) without significant loss of viability (Georgis, 1990; Nilsson & Gripwall, 1999; Fife *et al.*, 2003). Water-dispersible granule formulations of *S. carpocapsae*, which have a longer shelf life and are easy to mix and apply, have been commercially developed (Georgis & Dunlop, 1994). Nematodes are commonly applied at concentrations in the range 10^2–10^4 IJ ml^{-1} until spray runs off the target area to ensure maximum coverage. Nematodes may also be applied by drip and sprinkler irrigation systems, although the large droplet sizes and limited coverage associated with such techniques may limit the value of such systems as a foliar application technique (Georgis, 1990).

In this paper, the potential of entomopathogenic nematodes in novel environments is addressed using a general linear model. Studies collated from the literature were used to test for patterns in the efficacy of nematode applications in the management of above-ground pests. The focus is on field and greenhouse assessments, rather than laboratory-based assays where relevant ecological barriers to infection are typically removed. With reference to case studies, the model is used to help interpret the relative importance of different factors and highlight priorities for workers considering using entomopathogenic nematodes to target pests in novel environments.

Materials and methods

Noting broad variability in the case studies reported in the literature (table 1), our objective was to determine which factors explained the greatest amount of variation in the efficacy of entomopathogenic nematodes in the management of above-ground pests. An initial database comprising 207 studies was compiled from 29 peer-reviewed research articles selected from table 1. The remaining studies did not contain adequate data for analysis. To improve statistical power, multiple trials reported by the same authors were included provided they were conducted and analysed separately. The data collected included three groups of nematodes (*S. carpocapsae*, *S. feltiae*, *Heterorhabditis* spp.) applied to control pests in different habitats (exposed foliage, cryptic foliage or stem/trunk boring) and locations (greenhouse or field). The application conditions (temperature and relative humidity up to 8 h post-application), use of spray additives (surfactants or anti-desiccants) and nematode dosage (both concentration (IJ ml^{-1}) and occasions when sampling followed consecutive applications 3–4 days apart) were also noted. Factors including wind speed, solar radiation, time of applications, rainfall and strain of nematode used were not always reported and therefore not included in the analysis. As the dependent variable, either the proportion of hosts infected or the reduction in the target populations when control mortality remained $< 20\%$ was used, depending on the methods of assessment employed. In cases with repeated sampling, the highest reported rate of infection/mortality (within 5 days of treatment) was used in the analysis.

Because the database contained both ordinal (categorical but ordered) and interval (continuous) data, analysis of variance and linear regression could not be used. A general linear model that can evaluate multiple factors including ordinal and interval factors simultaneously (Neter *et al.*, 1996) was therefore chosen. Scatter plots of efficacy (infection rate) versus other variables were used to examine the nature of relationships (e.g. linear, quadratic), to detect outlying data or possible interactions. This exploratory step suggested that the groups of nematodes may show different relationships to the independent variables. Consequently, a single model (SAS Institute (1999); PROC GLM) was used for the most commonly used species, *S. carpocapsae*, (used in 136 independent trials) to test for the effects of application methods, abiotic conditions, and pest habitat on the post-treatment infection rate. Results for continuous variables were interpreted similarly to those of linear regression; a significant *F*-test indicates a relationship between dependent and independent variables and the sign of the slope (+ or −) defines the nature of the relationship. For categorical variables, effects are also detected using a simple *F*-test, but least-squares estimated means (LS means) and standard errors of infection rates were separated using a simple *t*-test. Because not all influential factors can be incorporated into the model, the aim of this approach was not to predict the effectiveness of nematode applications under a given situation, rather to reveal trends in efficacy and highlight priorities for using entomopathogenic nematodes to target pests in novel environments.

Results and Discussion

The use of nematodes as inundative bioinsecticides against above-ground pests have favoured *S. carpocapsae*, which was also referred to between 1983 and 1990 as *S. feltiae* Filipjev. *Steinernema carpocapsae* occurs naturally near the soil surface (Kaya, 1990; Campbell & Gaugler, 1993) and appears

Table 1. Field and greenhouse trials using entomopathogenic nematodes against insect pests in different above-ground environments.

Pest habitat	Target(s)	Location	Reference(s)
Exposed foliage	Colorado potato beetle; *Leptinotarsa decemlineata* Say	Field grown potato	Welch (1958), Welch & Briand (1961b), Macvean *et al.* (1982)
	Hymenopteran sawflies; *Cephalcia lariciphila* Wachtl (Pamphiliidae), *Hoplocampa testudinea* Klug (Tenthredinidae)	Commercial larch and apple stands	Georgis & Hague (1988), Vincent & Bélair (1992), Bélair *et al.* (1998)
	Diamondback moth, *Plutella xylostella* Linnaeus (Plutellidae)	Hawaiian watercress farms and greenhouse radishes	Baur *et al.* (1997a, 1998)
	(Other Lepidoptera)		
	Heliothis virescens Boddie (Noctuidae), *Pieris rapae* Linnaeus (Pieridae), *Diaphania hyalinata* Linnaeus (Pyralidae)	Field row crops (tobacco, cabbage, cucurbit)	Chamberlin & Dutky (1958), Welch & Briand (1961a), Shannag & Capinera (1995)
	Operophtera brumata Linnaeus (Geometridae), *Hyphantria cunea* Drury (Arctiidae)	Trees in apple and cherry orchards	Jaques (1967), Yamanaka *et al.* (1986)
	Heliothis armigera Hübner, *Spodoptera littoralis* (Boisduval) and *Earias insulana* Boisduval (Noctuidae)	Greenhouse-grown bean seedlings and two-month-old cotton plants	Glazer & Navon (1990), Glazer *et al.* (1992)
	Beet armyworm, *Spodoptera exigua* Hübner (Noctuidae)	Infested nursery ornamentals	Begley (1990)
Cryptic foliage	(Lepidoptera: Tortricidae)		
	Oblique banded leafroller *Choristoneura rosaceana* Harris	Apple orchard	Bélair *et al.* (1999)
	Western spruce budworm, *Choristoneura occidentalis* Freeman	Grand fir plantations; 2–3 m, *Abies grandis* (Dougl.) Lindl.	Kaya *et al.* (1981), Kaya & Reardon (1982)
	Spruce budmoth, *Zeiraphera canadensis* Mutuura & Freeman	White spruce plantations	Eidt & Dunphy (1991)
	Codling moth, *Cydia pomonella* Linnaeus	Cardboard bands placed around apple tree trunks	Kaya *et al.* (1984), Unruh & Lacey (2001)
	Leafminers (Diptera: Agromyzidae)		
	Liriomyza huidobrensis Blanchard, *L. trifolii* Burgess	Protected ornamental and vegetable crops (lettuce, cabbage, tomato and chrysanthemum)	Harris *et al.* (1990), Hara *et al.* (1993), Broadbent & Olthof (1995), Williams & MacDonald (1995), Williams & Walters (2000), Head *et al.* (2002)
Stem and cornboring Lepidoptera	*Ostrinia nubilalis* Hübner (Crambidae)	Sweet corn grown in a screenhouse	Ben-Yakir *et al.* (1998)
	Helicoverpa zea Boddie (Noctuidae)	Artificial and natural infestations on field grown corn	Bong & Sikorowski (1983), Bong (1986), Richter & Fuxa (1990)
	Eldana saccharina Walker, *Eoreuma loftini* Dyar (Pyralidae)	Field-grown sugarcane	Spaull (1992), Legaspi *et al.* (2000)
	Platyptilla carduidactyla Riley (Pterophoridae)	Artichoke leaf stalks and flower buds	Bari & Kaya (1984)
Wood-boring insects	*Euzophera semifuneralis* Walker (Pyralidae)	Stone fruit trees	Kain & Agnello (1999)
	Clearwing borers, *Synanthedon exitiosa* Say, *S. myopaeformis* Borkhausen (Sesiidae)	Peach and apple orchards	Deseö & Miller (1985), Cossentine *et al.* (1990), Nachtigall & Dickler (1992)
	S. culiciformis Linnaeus and *S. resplendens* Edwards (Sesiidae)	Alder and sycamore stands	Kaya & Brown (1986)
	Currant clearwings, *S. tipuliformis* Clerck (Sesiidae)	Cane cuttings and established plantings of blackcurrants	Bedding & Miller (1981), Miller & Bedding (1982)
	Prionoxystus robinae Peck (Cossidae)	Artificially infested harvested oak timber	Forschler & Nordin (1988)
	Scolytus scolytus Fabricus (Scolytidae)	Naturally infested harvested elm logs	Finney & Walker (1979)

better able to tolerate desiccation than other species (Simons & Poinar, 1973; Glazer & Navon, 1990; Kung *et al.*, 1991; Koppenhofer *et al.*, 1995). Model results for variables potentially impacting performance of *S. carpocapsae* are shown in table 2.

Among eight factors tested, the target habitat explained most variance. The results show a significant trend of efficacy increasing with degree habitat concealment; LS means for infection rate were 34% higher among borers (representing a 65% increase) compared with exposed foliar pests, with cryptic foliar pests falling in-between (fig. 1). Location was also highly significant; LS means were 17% higher (30% increase) among trials conducted in glasshouses compared with field sites (fig. 2). The model also indicated environmental conditions during or shortly after application influenced the effectiveness of nematode treatments. Figure 3 illustrates the trend with continuous data and shows the linear relationships between the residuals and both increasing r.h. (relative humidity) and temperatures (over the range 45–100% and 8–30°C respectively) when data from other factors are included in the model. Spray adjuvants including several commercial formulations with claimed spreading and evaporation retarding properties (wetting agents or anti-desiccants) are routinely included in an attempt to improve nematode performance. However, any benefits of using either surfactants or antidesiccants in formulations were not apparent in the model results (table 2). It is similarly notable that the concentration of nematodes applied (IJ ml^{-1}) was not significant. Moreover, although LS means among pests that had been sampled following consecutive applications of nematodes 3–4 days apart were higher than for single applications (74 vs. 62%), the model did not reveal a statistical improvement.

Model interpretation

The model described based on research data predicts that best targets for entomopathogenic nematodes above the ground are pests in cryptic habitats and protected locations (such as greenhouses), especially where aided by favourable environmental conditions during and shortly after application. While, in practice, each situation poses a more complex set of challenges, the relative importance of different factors and promising directions for future research are briefly discussed.

Target habitat and location

The leaf surface provides the greatest challenge by maximizing nematode exposure to air movement, sunlight, and low relative humidity that result in rapid desiccation and death (Gaugler *et al.*, 1992; Smits, 1996; Fujiie & Yokoyama, 1998). For this reason, most efforts to use nematodes for short-term control of exposed foliage feeders have failed and the high levels of virulence commonly observed in laboratory assays have not been repeated against a range of pests within the canopy (table 1). For example, in both Hawaii and Malaysia, the feasibility of using foliar nematode sprays of *S. carpocapsae* All strain and *Heterorhabditis* sp. against *Plutella xylostella* L. (Plutellidae) larvae could not be demonstrated, despite the selection of the most efficacious strains, formulations and doses and applying nematodes in the evening in humid cropping systems (Baur *et al.*, 1998; Mason *et al.*, 1999). In field tests against sawflies, foliar sprays of *S. carpocapsae* plus 10% glycerin infected 3–29% of larvae of *Cephalcia lariciphila* Wachtl. (Hymenoptera: Pamphiliidae), despite the bagging of treated branches to attempt to increase the persistence of IJ (Georgis & Hague, 1988). In another study, Shannag & Capinera (1995) evaluated evening applications of the *S. carpocapsae* All strain against the melonworm, *Diaphania hyalinata* Linnaeus (Lepidoptera: Pyralidae), feeding foliage of field-grown squash. Field applications of 5 billion nematodes per hectare under optimum environmental conditions produced infection rates of 52–55% but the rapid death of remaining nematodes the following morning prevented economic control.

Table 2. Results of general linear model (PROC GLM) of the performance of *Steinernema carpocapsae* applied against insect pests in above-ground environments under different pest habitats, study locations, application conditions and dosages.

Source	df	Type III SS	*F*	*P*
Habitat	2	8606	10.01	< 0.0001
Location	1	5033	11.71	0.0009
Relative humidity	1	3730	8.68	0.0041
Temperature	1	2250	5.23	0.0244
Antidesiccant	1	1337	3.11	0.0811
Repeat application	1	860	2.00	0.1606
Dose (IJ ml^{-1})	1	664	1.54	0.2171
Wetting agent	1	0.05	0.00	0.9914

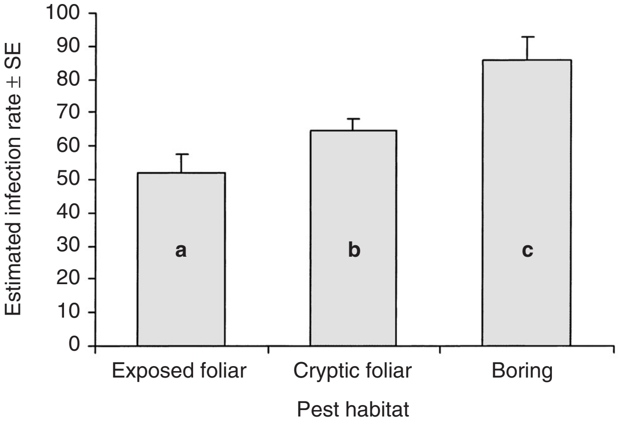

Fig. 1. Host infection rates of *Steinernema carpocapsae* applied to control pests across three habitat types. Data shown are estimated least squares means for each habitat separated by a *t*-test while evaluating other variables simultaneously (see table 2). Columns labelled with different letters are significantly different; $P < 0.05$.

The relationship between nematode efficacy and degree of habitat concealment (table 2, fig.1) supports the hypothesis that among foliar pests, those occupying cryptic habitats are preferred targets because infective stage juveniles are to some degree protected in their target site. Nematode activity would be promoted by the maintenance of surface moisture and elevated humidity following applications. As a complementary factor, environmental mediation may explain the apparent better performance of nematodes applied in protected structures (notably greenhouses) compared with field crops (fig. 2).

Although many pests in both cryptic foliar habitats and greenhouses have not been adequately controlled using nematodes, encouraging results have been obtained, notably

Fig. 2. Host infection rates of *Steinernema carpocapsae* applied against above-ground pests in protected and field crops. Data shown are estimated least squares means for trial location separated by a *t*-test while evaluating other variables simultaneously (see table 2). Columns labelled with different letters are significantly different; $P < 0.05$.

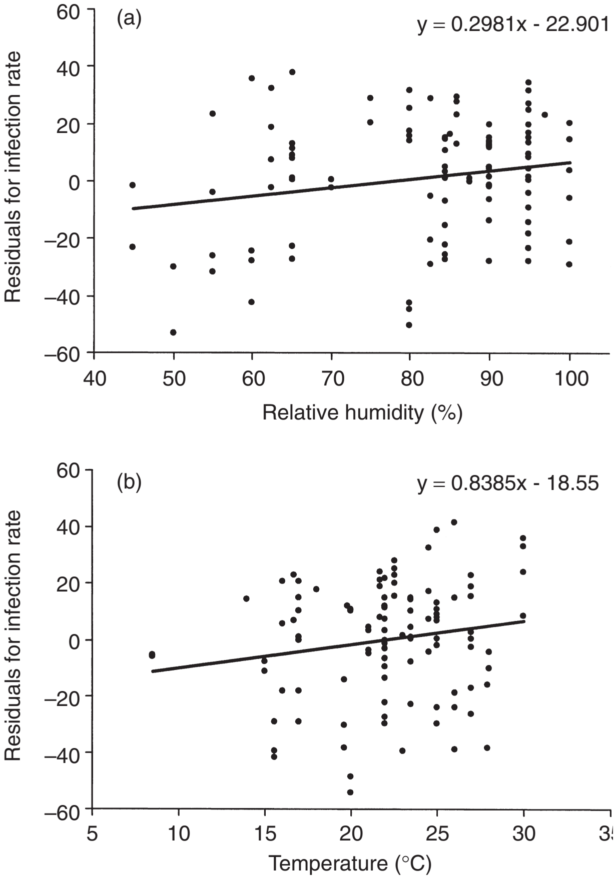

Fig. 3. Scatter plots of (a) relative humidity and (b) temperature at the time of nematode application, against model residuals (observed minus predicted host infection rates of *Steinernema carpocapsae* applied against above-ground pests). Plotted lines show the linear relationships between the residuals and relative humidity or temperature when data from other variables are included in the model (see table 2).

in studies against a range of tortricids and leafminers, cosmopolitan pests of many fruit and nursery crops respectively (Parrella, 1987; Cross *et al.*, 1999). For example, research indicates good control potential for *Steinernema* spp. and *Heterorhabditis* spp. for suppression of overwintering codling moth, *Cydia pomonella* Linnaeus (Lepidoptera: Tortricidae), when adequate moisture is maintained and temperatures are above 15°C (Kaya *et al.*, 1984; Nachtigall & Dickler, 1992; Unruh & Lacey, 2001). In the UK, a commercial formulation of *S. feltiae* (Nemasys®) has been tested as a foliar treatment against *Liriomyza huidobrensis* Blanchard (Diptera: Agromyzidae) infesting protected ornamental and vegetable crops. Good rates of control (> 80% larval mortality) were achieved under conditions of high (> 80%) humidity and moderate temperature on lettuce, cabbage and tomato (Williams & MacDonald, 1995; Williams & Walters, 1994, 2000; Head *et al.*, 2002). Such levels of control compare favourably with chemical pesticides (Williams & Walters, 2000). As a result of commercial interest, a strain of *S. feltiae* (Nemasys®) is currently marketed in the UK as a high volume foliar spray for western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae) (Pergande) infesting protected ornamental and bedding plants. Several UK growers of chrysanthemums and other potted plants are now using weekly sprays of *S. feltiae* for preventative control (Wardlow, 2002), although supporting quantitative data are lacking.

However, among Lepidoptera, overall best rates of control were obtained against larvae boring into layers of bark and cambium. Larval boreholes provide environments where nematodes may locate and infect host larvae while protected from hostile abiotic conditions. For woodboring species, two application strategies are commonly described. In bark surface treatments, nematodes are sprayed over the entire trunk and may be concentrated around heavily infested areas. Direct gallery injections apply suspensions to gallery openings with a stream nozzle or squirt bottle, are also effective but laborious and therefore less commonly used. Using such approaches, good rates of control (≥ 80%) have been reported for clearwing moths (Sesiidae), including *Synanthedon exitiosa* (Say) (Cossentine *et al.*, 1990), *S. culiciformis* Linnaeus (Kaya & Brown, 1986), *S. myopaeformis* Borkhausen (Deseö & Miller, 1985; Nachtigall & Dickler, 1992) and *S. tipuliformis* (Clerck) (Bedding & Miller, 1981; Miller & Bedding, 1982). In general, more limited success has been seen against stem- and cornboring Lepidoptera among the Pyralidae and Noctuidae, where reported control has tended to be low, inconsistent or not considered cost-effective (Bari & Kaya, 1984; Bong, 1986; Richter & Fuxa, 1990; Spaull, 1992; Ben-Yakir *et al.*, 1998; Legaspi *et al.*, 2000).

Environmental conditions

It is well established that relative humidity and temperature influence the effectiveness of entomopathogens under field conditions (Fuxa, 1987). Low moisture and high or low temperatures are commonly cited for nematodes failing to adequately control soil pests (Klein, 1990). Thus against above-ground pests, nematode applications should be timed during favourable conditions.

Studies on both foliage and bark surfaces show a minimum 8–24 h of elevated relative humidity (> 90%) is needed for high infection rates, but often a severe reduction in the activity of IJ occurs within 3–4 h exposure to reduced humidity (Glazer & Navon, 1990; Mason & Wright, 1997; Lacey & Unruh, 1998). Rainfall may provide an important source of water, although advantages need to be weighed against the risk of washing infective stage juveniles away from the target site, which has been cited as a possible problem (Kaya & Reardon, 1982). Suggested management strategies to minimize desiccation include spraying during the evening and using supplemental wetting prior to or following application. For example, both nematode survival and control of Colorado potato beetle *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) were enhanced following evening sprays compared with daytime applications (Macvean *et al.*, 1982). Unruh & Lacey (2001) demonstrated that lightly irrigating treated areas both one-half hour before and up to 24 h following treatment allowed nearly 100% infection of codling moth pupae in cardboard strips or logs attached to tree surfaces, compared with about 80% and 50%, when irrigating only once or not at all.

Steinernema carpocapsae possess an intermediate and relatively narrow thermal reproductive niche breath of 20–30°C with a reproductive optimum at 25°C (Grewal *et al.*, 1994). Application during conditions outside of this range will result in sub-optimum performance. However, considerable inter- and intraspecific variability in tolerances to abiotic stresses have been documented among entomopathogenic IJ. For example, *S. feltiae* is a cold adapted species, reproduces between 12–25°C, with reproductive optimum at 18°C while *S. riobrave* Cabanillas, Poinar & Raulston (Steinernematidae), reported from the Rio Grand Valley in Texas (Cabanillas *et al.*, 1994), is a warm adapted species reproducing at up to 35°C (Grewal *et al.*, 1994). Thus selection of nematodes should be appropriate for the locations.

Formulations and adjuvants

In addition to silicone and resin-based spreading and sticking agents, additional products to retard evaporation, such as mineral waxes, are now commercially available. Studies using a range of such additives in aqueous nematode suspensions have shown increased deposition on foliage (Mason *et al.*, 1998b), prolonged survival and improved control by nematodes compared with water alone (Macvean *et al.*, 1982; Shapiro *et al.*, 1985; Glazer *et al.*, 1992; Broadbent & Olthof, 1995; Baur *et al.*, 1997a). However, the overall benefits of using antidesiccants or general wetting surfactants were not apparent in the model results (table 2). Such an observation may reflect the wide range of products tested, some of which were reported ineffective, inappropriate for the situation or on occasions nematicidal, rather than the lack of any specific benefit. Although infrequently tested, including solar radiation protectants in formulations may well be beneficial in areas of high UV. Commercially available 'Blankophor fluorescent brighteners' have been shown to preserve up to 95% infectivity of *S. carpocapsae* All strain after 4 h of exposure to direct sunlight although other Blankophors were not as effective (Nickle & Shapiro, 1994). It appears that the benefits of formulation additives are best tailored to specific scenarios.

Nematode dose

While some studies included in the model reported dose-dependent infection rates (Glazer *et al.*, 1992; Spaull, 1992), nematode concentration (IJ ml^{-1}) was not associated with efficacy in the model. Moreover, consecutive applications of nematodes 3–4 days apart did not improve infection rates statistically, although if pests were removed from the target site it is possible that initial mortality (following first application) may have been underrepresented. While the model power does not support specific conclusions, a general interpretation is that applying more nematodes in response to low rates of control is unlikely to adequately compensate for other limiting factors, such as rapid death of infective stages at the target site. Conversely, under ideal conditions for nematodes, relatively low doses (i.e. that are economically feasible) may be effective.

Other considerations for research

The model's predictions regarding the relative importance of different factors on the performance of nematodes provide general guidelines for future workers interested in exploiting the potential of entomopathogenic nematodes in non-traditional environments. However, additional factors not included in the analysis above can influence the effectiveness of nematode applications above-ground; three important examples of which are noted below.

Application techniques

It has been recently noted that there are few guidelines on how entomopathogenic nematodes should be formulated and applied to optimize their performance (Fife *et al.*, 2003; Gan-Mor & Matthews, 2003). Although general practice restricts the application of most biopesticides to conventional agricultural spray equipment (Georgis, 1990), there may be value in developing alternative application methods. For example, a hydraulic spray gun used to concentrate nematode suspensions close to trunks produced higher infection rates of codling moth larvae than the more commonly used but less focused air blast sprayer (Unruh & Lacey, 2001). In developing countries, battery-operated spinning disc sprayers are a cheap alternative for resource-poor farmers. In comparative tests, spinning discs gave nearly 50% mortality of *P. xylostella* larvae on cabbage while applying less than 9% of the nematodes that were applied using hydraulic nozzles (Lello *et al.*, 1996), suggesting that further work on low volume systems maybe economically justified. Using nematode-impregnated collars placed around hibernation sites on tree surfaces also provides a novel slow-release system against various orchard pests (Kaya *et al.*, 1984; Nachtigall & Dickler, 1992). The use of pre-desiccated formulations of nematodes requires special care when used to target above-ground pests. For example Baur *et al.* (1997b) demonstrated the efficacy of a wettable granule (WG) formulation of *S. carpocapsae* against *P. xylostella* was reduced unless nematodes were rehydrated for 48 h prior to use. The choice of application method may influence how nematodes should be formulated for best results.

Selection of entomopathogenic nematode strains

As noted above, different species of entomopathogenic nematodes have distinct temperature niches for activity and may also respond differently to moisture availability (Kung *et al.*, 1991; Brown and Gaugler, 1997). Despite the obvious benefits of selecting the most favourable nematode for a particular job, the current availability of commercial species and strains restricts the grower to a limited selection. Therefore, there may be value in encouraging cottage industry production of local species and strains for use in specific environments. Selective breeding through serial passage or hybridization can increase temperature tolerances (Grewal *et al.*, 1996; Shapiro *et al.*, 1997) and may improve other desirable traits such as enhanced host finding (Gaugler & Campbell, 1991; Jansson *et al.*, 1993) without the need for the extensive testing associated with transgenic strains. A selection for desiccation tolerances could predispose strains for use in foliar sprays, although the costs associated with commercial investment may limit the practicality of such approaches.

Insect parasitic nematodes

While current pest management research heavily emphasizes rhabditids in the genera *Steinernema* and *Heterorhabditis*, species of nematodes among the Phaenopsitylenchidae, Mermithidae, Sphaerulariidae, Tetradonematidae, Parasitylenchidae and Allantonematidae have been recovered from hosts in the Coleoptera, Diptera, Thysanoptera, Lepidoptera and Hymenoptera (Kaya, 1993; Kaya & Stock, 1997). Although these nematodes carry no mutual bacteria and rarely cause rapid host mortality, they often form intimate, highly adapted parasitic relationships and thus are not naturally restricted to soil-dwelling stages. Mermithids have attracted some attention as potential biological control agents of mosquitoes because they may reach high densities in host populations, and almost always kill their host. However, to date, the lack of effective *in vitro* rearing procedures has prohibited the use of parasitic nematodes in inundative strategies. As an alternative, parasitic nematodes may be released in inoculative strategies, although their value as biocontrol agents remains uncertain.

Conclusions

The expanded commercial use of nematodes as bioinsecticides still emphasizes soil applications, although recent research suggests that in some cases applications against foliar or wood boring pests may be feasible. Successful use requires that the ecology of the target is matched to the activity of infective juveniles; in practice, targets are protected from environmental extremes, applications are timed to coincide with susceptible host stages and favourable weather conditions and nematodes are able to rapidly locate and infect hosts. For now, species of woodboring Lepidoptera appear the most promising targets for above-ground applications of nematodes, although foliar sprays of nematodes have also shown promise against pests including tortricids, leafminers and stemborers in a variety of settings. Issues including resistance and restrictions to current pesticides and the lack of effective biological control alternatives make using nematodes against such a range of foliar pests of tree fruit, nursery and vegetable crops desirable. However, in addition to performance, factors including cost, availability, environmental conditions, compatibility within integrated strategies and alternative options for organic growers will ultimately determine the extent to which nematodes are used against above-ground pests

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