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Effects of Insecticides on Movement, Nictation, and Infectivity of *Steinernema carpocapsae*[1]

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Abstract: Movement, nictation, and infectivity of *Steinernema carpocapsae* strain All were compared for ensheathed (EnJ) and desheathed (DeJ) infective juveniles exposed to the insecticides acephate, dichlorvos, methomyl, oxamyl, or permethrin. Nematode response to various solutions included normal sinusoidal movement, uncoordinated motion, twitching, convulsion or formation of a pretzel shape, an inactive "S" posture with fine twitching, or a quiescent straight posture. The DeJ displayed these movements at lower concentrations of each insecticide than did EnJ. In petri dish bioassays, insecticide-treated EnJ caused generally lower mortality in the common cutworm, *Spodoptera litura,* than did EnJ alone but caused greater insect mortality than did insecticides alone. Nematode response to chemicals was more clearly demonstrated by nictating behavior than by the movement bioassay. Nictation of DeJ was suppressed by the test chemicals at low concentrations, except for acephate and permethrin. Nictating EnJ or DeJ, regardless of chemical treatment, killed host insects faster than did non-nictating juveniles. Insecticides that enhance nictating behavior at certain concentrations may be used for mixed applications with nematodes.

Key words: acephate, behavior, dichlorvos, entomopathogenic nematode, infective juvenile, insecticide, methomyl, mixed application, movement, nematode, nictation, oxamyl, permethrin, *Spodoptera litura, Steinernema carpocapsae.*

Entomopathogenic nematodes from the Steinernematidae and Heterorhabditidae are promising biological alternatives to chemical insecticides (15,20,28). These nematodes can penetrate and kill many economically important pests within 24–48 hours (28). The field efficacy of these nematodes remains limited, however, because of their vulnerability to environmental extremes, such as low humidity or solar radiation (7,8,28), and because of their tendency to become immobile in soil after application (9,17). On the other hand, steinernematid nematodes are relatively insensitive to many agricultural chemicals, e.g., insecticides (2,4,5,11,30,32,33), fungicides (2,32,33), or herbicides (3,6,30,32, 33). This chemical compatibility indicates a potential for combined applications of nematodes with chemicals (14,16). An additional possibility is that such chemicals may stimulate passive or inactive nematodes and thereby enhance their infectivity against the target insects. In field trials, a mixed application of *Steinernema carpocapsae* with certain insecticides has provided more effective insect control than separate applications of each (12,13,16).

In contrast to field studies, treatment with organophosphate and carbamate pesticides has impaired the infectivity of *S. carpocapsae* under laboratory conditions (9–11,14,21), even though the infective juveniles were more active in the presence of these compounds. It was suggested, therefore, that such compounds may be toxic to *S. carpocapsae* applied to soil (10,11). Clearly, the discrepancy between laboratory and field tests requires further investigation from the viewpoint of nematode behavior when exposed to such chemicals.

This paper reports the effects of several insecticides on movement and infectivity of *S. carpocapsae* infective juveniles. Both ensheathed and desheathed juveniles were examined because of the expectation that most nematodes applied to soil would undergo exsheathment (or desheathment) as they moved, in contrast to those applied on above-ground plant surfaces, most of which remain ensheathed.

MATERIALS AND METHODS

Nematodes: Steinernema carpocapsae strain All from Biosys (Palo Alto, CA) was culti-

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vated on chicken offal medium with symbiotic bacteria for 1 month at 25 C (23). Nematodes isolated from the medium were immersed in 1% sodium dodecyl sulfate for 20 minutes to recover only infective juveniles. After being centrifuge-washed five times with distilled water, the infective juveniles were passed through a 30-μm-pore nylon mesh to obtain ensheathed juveniles (EnJ). Some EnJ were treated with 0.1% NaOCl for 20 minutes and centrifuge-washed (450 *g*, 3 minutes) three times with distilled water to produce desheathed juveniles (DeJ). The DeJ were then passed through a 30-μm-pore nylon cloth and left in distilled water for 24 hours before use.

Insecticides: The insecticides used were oxamyl (methyl N',N'-dimethyl-N-[(methylcarbamoyl)oxy]-1-thiooxamimidate), technical grade 42.5% w/v (Sankyo Co. Tokyo, Japan, obtained from DuPont); acephate (O,S-dimethyl N-acetylphosphoramidothioate), 50% (w/w) a.i. wettable powder (Ortran, Sankyo Co., Tokyo); dichlorvos (dimethyl 2,2-dichlorovinyl phosphate) 50% (w/v) a.i. emulsifiable (xylene) concentrate (Des, Sankyo Co.); methomyl (S-methyl N-[(methylcarbamoyl)oxy]thioacetimidate) 45% (w/w) wettable powder (Lannate, Nihon Noyaku Co., Osaka, Japan); and permethrin (3-phenoxybenzyl d, l-*cis,trans*-3-(2,2-dichlorovinyl)-2,2-dimethylcyclopropanecarboxylate), 20% (w/v) a.i. emulsifiable (xylene) concentrate (Adion, Sankei Kagaku Co. Kagoshima, Japan). Stock solutions of these chemicals were freshly prepared in distilled water.

Movement of infective juveniles: About 1,000 EnJ or DeJ were placed in a 5.5-cm-d petri dish containing 4 ml of 0, 10, 50, 100, 200, 400, 800, or 1,000 μg/ml of each insecticide with three replications. After incubation for 0.5, 1, 3, 6, 12, and 24 hours at 25 C, ca. 100 individuals from each dish were transferred to a stereomicroscope, and their locomotion was recorded with a videocassette recorder for a few minutes at ×60. Nematode movement was analyzed under reduced speed (1/20) and grouped into six categories as a percentage of the total; sinusoidal undulation, a coiled and twisted pretzel shape, convulsion or violent twitching, uncoordinated movement between the anterior and posteior portions, inactive S-shaped posture, and inactive straight posture. The experiment was performed three times for both EnJ and DeJ.

Nictation: About 20,000 EnJ or DeJ were placed in a 6-cm-d petri dish containing 4 ml of 50, 100, 150, or 200 μg/ml of each insecticide or deionized water as a control, with three replications per treatment; then 2 g of bark compost (Linnai, Ohji Paper Co., Tokyo), previously dried at 170 C for 2 hours and sieved through a 1-mm-pore screen, was layered 4–5 mm deep. The dishes were incubated at 25 C in the dark. After 1, 2, 3, and 4 days, nictating nematodes on the top surface of the bark compost were counted in 10 randomly chosen stereomicroscopic fields (0.785 cm^2/field). Because the surface area of bark compost was 28.26 cm^2, the mean number of nictating nematodes was multiplied by 36 to obtain the total number of nictaing nematodes in a dish. Nictating nematodes were expressed as ratios relative to controls. The experiment was performed four or more times.

Infectivity of insecticide-treated infective juveniles: The ability of insecticide-treated EnJ or DeJ to cause host mortality was tested against starved last-instar larvae of *Spodoptera litura*. A single larva was placed on a 5.5-cm-d filter paper in a 5.5-cm-d petri dish containing 0.4 ml of nematode–insecticide suspension containing 0, 50, 100, 200, or 400 μg/ml of each insecticide and 10 nematodes per insect, based on the LC_{50} (for 2 days) of EnJ against these larvae (24). Ten replicates were used per treatment. The dishes (covered with lids but unsealed) were placed in the dark at 25 C. After 24 and 48 hours, the mortality of insect larvae was recorded. Nematode-free insecticide solutions were tested in parallel with the above experiment. The experiment was performed four times.

Infectivity of nictating juveniles: Infectivity was assessed by mortality of nematode-

inoculated insects. A nylon cloth sieve (125-μm aperture, 6 × 6 cm) was placed on the upper surface of 2 g dried bark compost in a 6-cm-d petri dish containing ca. 20,000 EnJ or DeJ with or without 4 ml of 50 μg/ml of each insecticide. After incubation for 24 hours in the dark at 25 C, the cloth sieve and the nictating nematodes on it were removed. The nematodes were rinsed from the cloth with distilled water in a 15-ml plastic centrifuge tube. Fifty EnJ or DeJ were immediately transferred with 0.4 ml distilled water to a filter paper in a petri dish (5.5-cm d) containing a last-instar larva of *S. litura*. This procedure was completed within 30 minutes after nematode release from the cloth. Non-nictating infective juveniles, which had been kept in water for 24 hours at 25 C, were also used in this bioassay. The percentage mortality of insects was recorded at 6-hour intervals from 18 to 48 hours and probit-converted to obtain LT_{50}. The experiment was performed three times with 10 replicates per treatment.

Statistical analysis: Percentages of locomotion patterns in each category were arcsine-transformed to ensure normality. Percentage of insect mortality was analyzed with contingency tables. Multiple comparisons were made with Duncan's multiple-range test. All comparisons used a 0.05 level of significance.

Results

Locomotion: In distilled water controls, 90% of the *S. carpocapsae* EnJ became quiescent and straight in 30 minutes, and 100% within 3 hours. In contrast, 30% of the DeJ remained actively moving 6 hours after incubation, i.e., after a total of 30 hours in distilled water, because the DeJ had been kept in distilled water for 24 hours after desheathment. All tested insecticides stimulated EnJ and DeJ to move actively, even after a 24-hour exposure, particularly dichlorvos, methomyl, and oxamyl. In 400-μg/ml solutions of these three chemicals, nearly 100% of EnJ (Fig. 1) and 80% of DeJ remained moving after 24 hours. Movement in these solutions was abnormal, however (Fig. 2). Although normal sinusoidal undulation occurred in solutions of oxamyl (50 μg/ml), acephate (100 μg/ml), and permethrin (50 and 100 μg/ml), a pretzel-twist posture was characteristic of nematodes in solutions of methomyl (100 μg/ml), oxamyl (200 and 400 μg/ml), and especially dichlorvos (10 μg/ml). Convulsion or violent twitching of EnJ occurred in solutions of methomyl (100 and 200 μg/ml). Uncoordinated move-

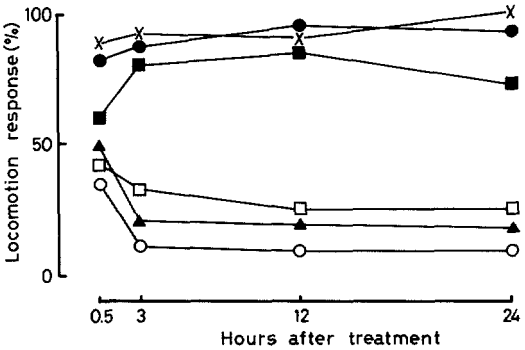

FIG. 1. Locomotory response (expressed as percentage of nematodes that are moving) of ensheathed infective juveniles of *Steinerema carpocapsae* exposed to 400 μg/ml oxamyl (●), dichlorvos (×), methomyl (■), permethrin (□), acephate (▲), or distilled water (○) as a control.

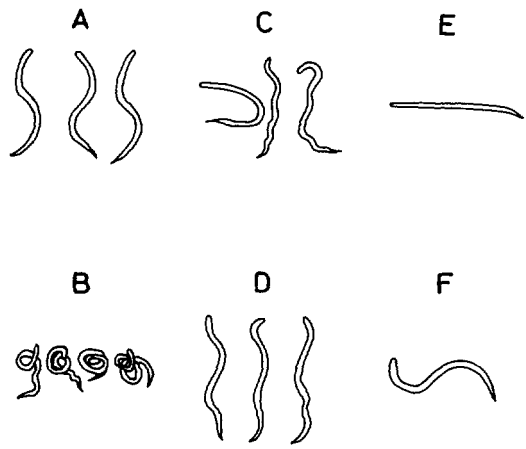

FIG. 2. Characteristic movements of *Steinernema carpocapsae* ensheathed infective juveniles (EnJ) in several insecticidal solutions. Movements were recorded 1 hour after treatment at 25 C. A) Sinusoidal undulation. B) Pretzel-twist shape. C) Convulsion or violent twitching. D) Uncoordinated movement. E) Inactive straight posture. F) Inactive "S" posture.

ment between anterior and posterior portions of nematodes was characteristic of 100 and 200 μg/ml solutions of oxamyl. All EnJ assumed an inactive, straight posture in solutions of 800 μg/ml or more oxamyl or an inactive "S" posture at 400 μg/ml or greater concentrations of methomyl, but these inactive nematodes treated with high concentrations of oxamyl or methomyl regained normal undulatory movements 24 hours after transfer to distilled water. Resumption of normal movement was seen in most juveniles treated with the test chemicals after transfer to distilled water.

In general, DeJ were more sensitive to the chemicals than EnJ. In contrast to the observed increase in sinusoidal undulation for EnJ in oxamyl at 10–50 μg/ml, DeJ in the same solutions adopted an "S" posture, with only anterior and posterior portions moving. In permethrin and acephate solutions, DeJ movement featured two phases that shifted 6 hours after incubation; the initial phase consisted of slow but large sinusoidal undulations accompanied by occasional convulsions; the later phase was characterized by an "S" posture with convulsions, especially at 200 and 400 μg/ml. In solutions of 200 and 400 μg/ml methomyl, the percentage of moving DeJ remained high (>80%), even after 24 hours; but movement was twitching or convulsive, and the DeJ adopted an "S" shape. Dichlorvos at 10 μg/ml produced a response similar to acephate or permethrin, with large undulations with occasional convulsions for 6 hours and then a characteristic pretzel posture after 12 hours. At concentrations ≥50 μg/ml, DeJ with twitching or pretzel postures appeared soon after the treatment commenced. Most (>70%) of the DeJ remained moving after a 24-hour exposure to 400 μg/ml dichlorvos, but movement was abnormal. The DeJ resumed normal body undulations after transfer to water following treatment with any of the tested chemicals.

Nictation: On day 1, 4–5% of the EnJ in distilled water controls nictated; this proportion increased linearly to ca. 10% on day 4. There was no difference ($P \geq 0.05$) in the nictation rate between control EnJ and DeJ. However, nictation rates of EnJ on day 1 were enhanced ($P \leq 0.05$) by 50-μg/ml concentrations of acephate, permethrin, and especially oxamyl (Fig. 3). However, the oxamyl-associated nictation rate declined precipitously on the next day. Acephate and permethrin at 100 and 200 μg/ml kept the nictation rates at nearly the same level as the control throughout the 4-day study. Methomyl and dichlorvos were obviously detrimental to nictation of EnJ, particularly dichlorvos (which entirely suppressed it, even at 50 μg/ml).

Nictation of DeJ was generally more sensitive to the tested insecticides than that of EnJ (Fig. 3). Methomyl and dichlorvos completely suppressed nictation even at the lowest tested concentrations. Oxamyl also had a strongly suppressive effect, whereas acephate at 50 μg/ml induced DeJ to nictate at a higher ($P \leq 0.05$) level on day 2 compared with the distilled water control. The nictation rates of DeJ treated with 100 or 200 μg/ml acephate or permethrin did not noticeably deviate ($P \geq 0.05$) from the control level during the 4-day study.

Infectivity: Mortality caused by EnJ was generally reduced when they were mixed with insecticides compared with nematodes alone, although EnJ in oxamyl, acephate, or permethrin at 50 or 100 μg/ml gave a slightly greater but not significant mortality ($P \geq 0.05$, Table 1). The mortality induced by DeJ (80% in 2 days, Table 2) was greater ($P \leq 0.05$) than that induced by EnJ. Oxamyl at all concentrations clearly suppressed the mortality caused by DeJ, and the mortality of insects in the 10-μg/ml oxamyl–DeJ mixture was greater than that caused by oxamyl alone. Mixtures of 10–200 μg/ml acephate with DeJ generally gave greater ($P \leq 0.05$) mortalities than the insecticides alone. However, these efficacies were at best equal to that of DeJ alone. Controls with distilled water alone gave no mortality during the experimental period.

The LT_{50} of nictating nematodes was 20.0 hours for EnJ and 22.5 hours for DeJ,

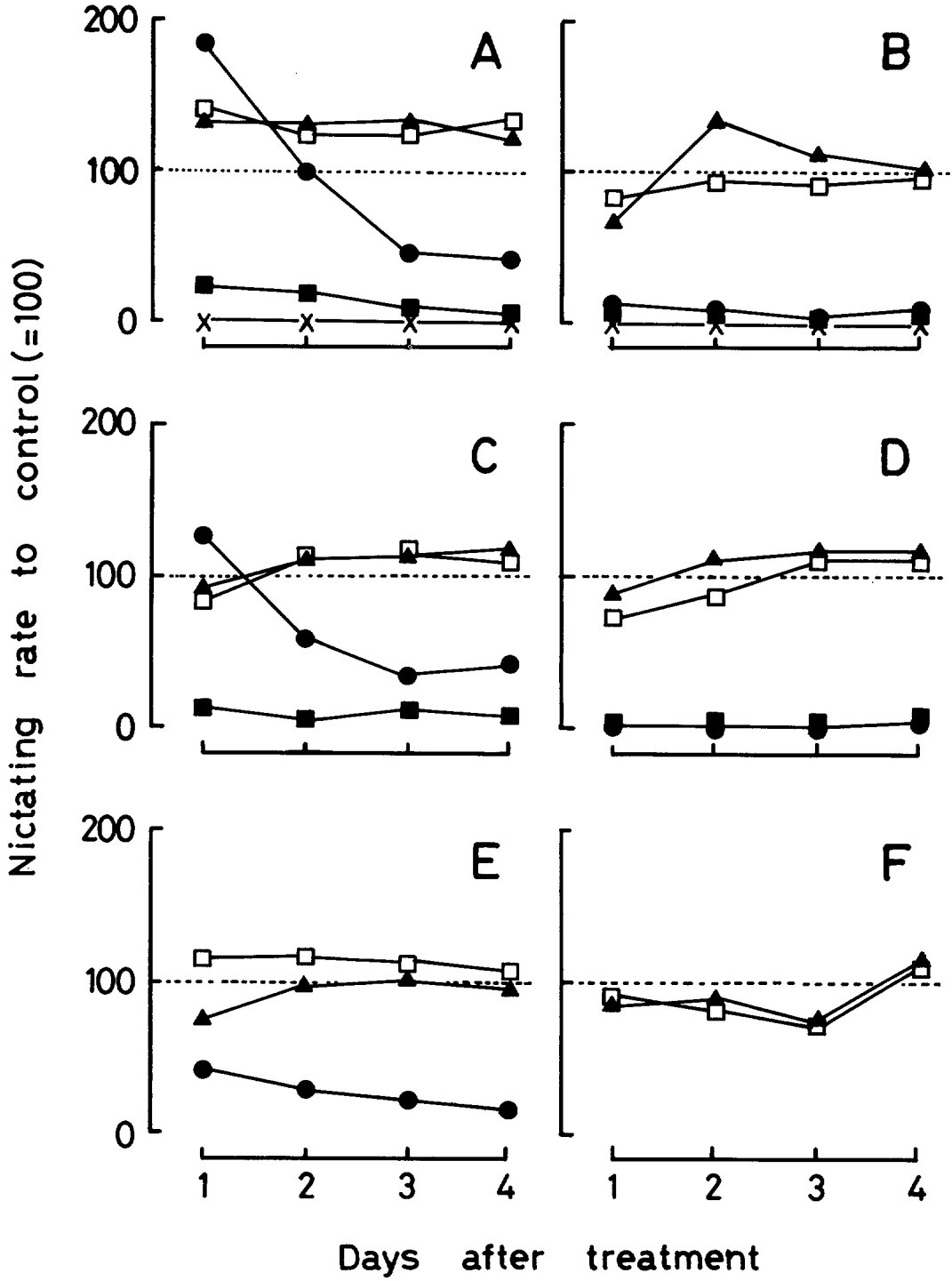

FIG. 3. Nictation of *Steinernema carpocapsae* infective juveniles as affected by several insecticides, expressed relative to distilled water control (=100). Treatments included oxamyl (●), permethrin (□), acephate (▲), methomyl (■), and dichlorvos (×). A) Ensheathed juveniles (EnJ), 50 μg/ml. B) Desheathed juveniles (DeJ), 50 μg/ml. C) EnJ, 100 μg/ml. D) DeJ, 100 μg/ml. E) EnJ, 200 μg/ml. F) DeJ, 200 μg/ml.

TABLE 1. Mortality (%) of starved last-instar larvae of the common cutworm, *Spodoptera litura*, caused by treatment with *Steinernema carpocapsae* strain All ensheathed juveniles (EnJ), insecticide solutions, and mixtures of both in petri dish bioassays.

		Insecticide alone (μg/ml)				Insecticide (μg/ml) plus EnJ			
Insecticide	EnJ alone	50	100	200	400	50	100	200	400
None	40–60 a								
Permethrin		20 b	45 a	48 a	50 a	50 a	60 a	68 a	50 a
Acephate		0	7 c	10 c	10 c	50 a	75 a	70 a	50 a
Oxamyl		0	0	0	10 c	50 a	70 a	50 a	40 a
Dichlorvos		0	0	0	0	5 c	5 c	5 c	5 c
Methomyl		5 c	10 c	20 b	25 b	50 †	20 b	20 b	25 b

Mortality was recorded 48 hours after treatment at 25 C. Ten EnJ (previously determined to be the LC_{50}) were used per insect. Values followed by the same letter are not significantly different ($P \leq 0.05$) according to Duncan's multiple-range test.
† Could not be analyzed because of large variance.

with no significant difference between them ($P \geq 0.05$), whereas the LT_{50} of non-nictating juveniles was 29.6 hours and 28.5 hours for EnJ and DeJ, respectively (Fig. 4). Nictating EnJ and DeJ, regardless of chemical treatment, killed host insects faster ($P \leq 0.05$) than did non-nictating juveniles, although all insect larvae were killed by nematodes of any experimental group within 48 hours of incubation (Fig. 5). The LT_{50} of nictating EnJ or DeJ collected from acephate or permethrin mixtures were the same ($P \geq 0.05$) as those unexposed to insecticides. The LT_{50} of nictating oxamyl-treated EnJ was 2 hours longer than that of other batches of nictating EnJ, although it was shorter ($P \leq 0.05$) than that of non-nictating EnJ unexposed to insecticide. There were so few nictating oxamyl-treated DeJ and nictating methomyl-treated EnJ and DeJ that these were not employed for this experiment. Nictating nematodes were not obtained from dichlorvos treatment.

DISCUSSION

All tested insecticides stimulated both EnJ and DeJ to move actively, although such movements were not necessarily normal. Compared to plant nematodes such as second-stage juveniles of *Meloidogyne incognita* (19,22), the infective juveniles of *Steinernema carpocapsae* were extremely tolerant to these compounds. The insecticide-stimulated movement did not always enhance mortality in the petri dish bioassays, however, and this finding does not support the premise that mixing nematodes with chemicals would synergistically improve insect control. Neverthless, effective field results have been obtained with mixed application of *S. carpocapsae* with diazinon, fenitrothion, dichlorvos, oxamyl, acephate, or permethrin, compared with applications of nematodes or insecticides alone (12–14,16). Sinusoidal undulation seemed to be the normal movement for infective juveniles. Gaugler and Campbell

TABLE 2. Mortality (%) of starved last-instar larvae of *Spodoptera litura* caused by treatment with *Steinernema carpocapsae* strain All desheathed infective juveniles (DeJ), insecticide solutions, and by mixtures of both in petri dish bioassays.

		Insecticide alone (μg/ml)				Insecticide (μg/ml) plus DeJ			
Insecticide	DeJ alone	10	50	100	200	10	50	100	200
None	80 a								
Acephate		13 a	10 b	23 b	30 b	77 a	80 a	73 a	86 ac
Oxamyl		13 b	13 b	23 b	23 b	73 a	20 b	20 b	30 b

Mortality was recorded 48 hours after treatment at 25 C. Ten DeJ were used per insect, based on LC_{50} of 10 EnJ. Values followed by the same letter are not significantly different ($P \leq 0.05$) according to a *t*-test.

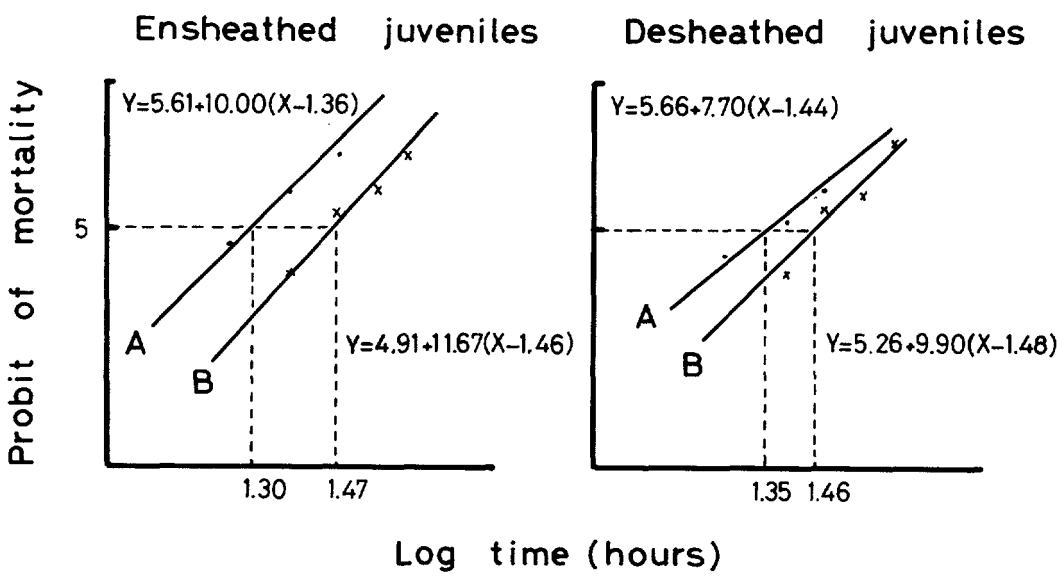

FIG. 4. Fifty percent lethal time (LT_{50}) for starved last-instar larvae of *Spodoptera litura* incubated with nictating (A) or non-nictating (B) infective juveniles of *Steinernema carpocapsae*.

(9) concluded that increased sinusoidal movement did not necessarily enhance host-finding behavior. Similarly, in the present experiments, a positive relationship between active movement and infectivity of nematodes did not occur.

Nictating behavior appears to be a better indicator than movement for screening pesticides for compatibility with nematodes. Soil moisture, which induces a high nictation rate, is correlated with high insect mortality (18,25,26). In our experiments, nictating infective juveniles killed cutworm larvae faster than did non-nictating juveniles. Nictating juveniles are also more attracted to insect plasma and penetrate the insect body more readily than non-nictating ones (Ishibashi et al., unpubl.). Any bioassay involving nictating juveniles should be conducted immediately after their collection, because they eventually become quiescent and adopt a straight posture within an hour after return to water. Chemically treated nictating juveniles, whether EnJ or DeJ, killed insect larvae faster than non-nictating juveniles untreated with chemicals. There was no significant difference in mortality caused by nictating EnJ and DeJ with or without insecticides. Therefore, we believe that nematodes could be successfully mixed with chemicals that enhance the nictating behavior of infective juveniles.

In contrast to our expectations, DeJ caused greater mortality of insects than EnJ. Campbell and Gaugler (1) found no difference in *Galleria mellonella* mortality caused by ensheathed versus desheathed *S. carpocapsae* juveniles; interestingly, *G. mellonella* larvae are more susceptible to *S. carpocapsae* than *S. litura* larvae. In our experiments, *S. litura* mortality caused by DeJ was 80% in 2 days, whereas EnJ gave ca. 50%. This difference may have resulted from greater movement of DeJ than EnJ, even in distilled water. Accordingly, the LC_{50} of DeJ may be lower than that of EnJ. Permethrin- or acephate-treated DeJ at concentrations from 10–100 μg/ml gave greater mortalities than did the insecticides alone, but these mortalities were only slightly better than that caused by DeJ alone. In contrast, oxamyl at ≥50 μg/ml obviously suppressed DeJ infectivity. In laboratory experiments, rather negative results have been reported on the efficacy of nematode–pesticide mixture (9–11,21). At best, mixtures had no more than

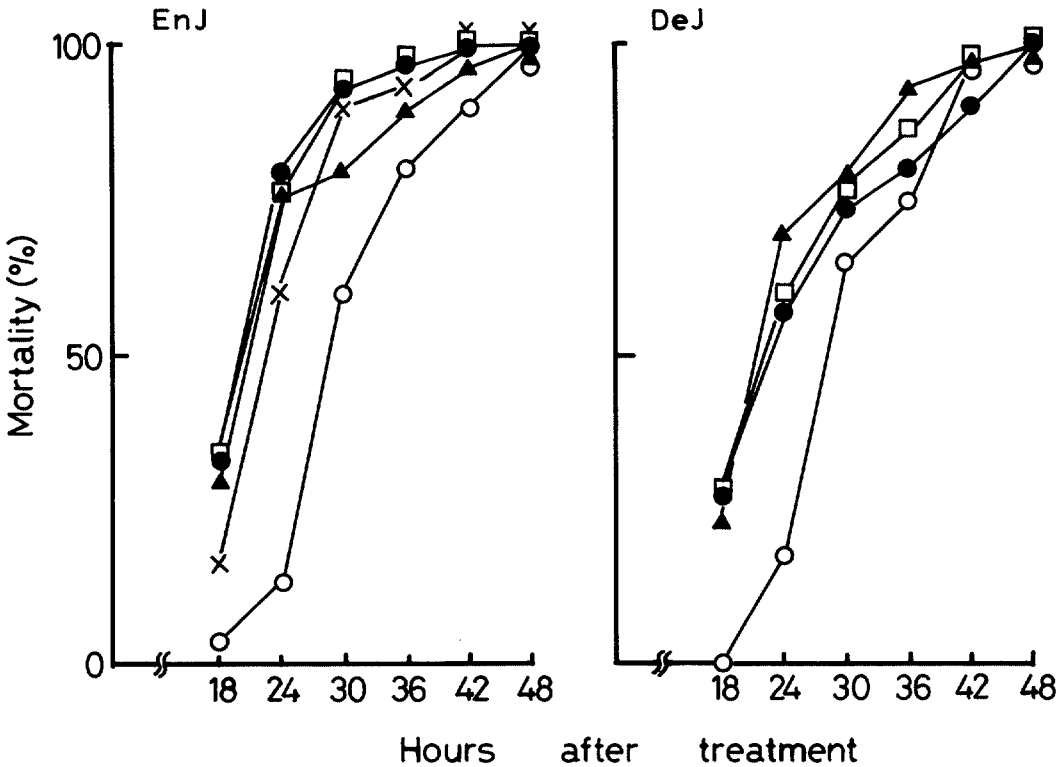

FIG. 5. Percentage mortality of last-instar larvae of *Spodoptera litura* incubated with nictating or non-nictating infective juveniles of *Steinernema carpocapsae*. Treatments included non-nictating juveniles obtained from aqueous suspension (○), nictating juveniles collected from bark compost immersed in water (●) or 50-μg/ml solutions of oxamyl (×), acephate (▲), or permethrin (□).

slightly better efficacy than nematodes alone. When the LC_{99} of infective juveniles is used, results of mixed applications are equal to or poorer than a single application of nematodes alone. Therefore, we suggest that the LC_{50} of infective juveniles should be employed to determine the synergistic effects of mixing with a chemical, the concentration of which should also be the LC_{50}. Fedorko et al. (5) estimated the LC_{50} of oxamyl to *S. carpocapsae* infective juveniles (probably ensheathed) to be 5,000 μg/ml. They calculated the concentration for practical co-application of oxamyl to range from 300–1,500 μg/ml and concluded that the lower doses of oxamyl recommended for plant protection do not constitute a serious threat to steinernematid nematode viability, even after prolonged exposure. This conclusion is supported by our unpublished field trials, in which mixed application of *S. carpocapsae* with oxamyl (Vydate [1.0% a.i. granular] at 35 kg/ha plus 1×10^6 nematodes/m^2) yielded better results than did a single application of each alone. Vydate at 35 kg/ha is a recommended dosage for soil application against root-knot nematodes. The oxamyl concentrations that enhanced nictating behavior were 10–50 μg/ml, far less than those suggested by Fedorko et al (5). Therefore, we believe that there is no concern about problems associated with the application of nematodes with insecticides or non-fumigant nematicides at their practical recommended dosages.

Steinernematid nematodes persist poorly on plant surfaces, because they are subjected to harsh conditions such as sunlight and low humidity. Therefore, foliarly applied nematodes should be activated to infect insects as fast as possible after appli-

cation. A suitable activator would be a nictation-enhancing compound like oxamyl, although the activator need not be an insecticide. For example, aloe or kale juice also activates infective juveniles (18). In contrast, *S. carpocapsae* applied to soil may survive relatively longer than when foliarly applied but is inclined to quiescence, adopting a straight posture (9,17,27). These quiescent nematodes were called "ambushers" by Gaugler et al. (9), who suggested that a high proportion of them would reduce the field efficacy of nematodes applied to soil. Accordingly, soil applications should include a compound to maintain nematode activity for a long time without having a detrimental effect on the nematodes. Acephate or permethrin would be possible examples, although these would not persist in soil.

Das and Divakar (2) and Prakasa et al. (29) demonstrated that ca. 15 insecticides had low toxicity to *S. carpocapsae* DD-136 and concluded that most insecticides can be used with this strain at practical concentrations. However, these results were based on nematode mortality, not on behavior or infectivity. In our experiments, dichlorvos stimulated nematode locomotion but even at a very low concentration it induced a pretzel conformation and entirely suppressed nictation and insect mortality in the petri dish bioassay. Nevertheless, we obtained good results in field trials for control of cabbage worms by mixed application of nematodes and dichlorvos (14). Laboratory bioassays are generally thought to provide better results than field tests, but we have observed the opposite.

We have not yet abandoned the idea of practical application of *S. carpocapsae* with compatible chemicals. Because sucking insects such as aphids or bugs are poorly controlled by nematodes, we expect that insecticides could compensate for the poor effectiveness of nematodes. More appropriate activators that do not harm nematodes may be discovered. Further studies should determine whether prior application of sublethal doses of insecticides facilitates nematode invasion and whether prior exposure to nematodes lowers insect resistance to insecticides.

Literature Cited

1. Campbell, L. R., and R. Gaugler. 1991. Role of the sheath in desiccation tolerance of two entomopathogenic nematodes. Nematologica 37:324–332.

2. Das, J. N., and B. J. Divakar. 1987. Compatibility of certain pesticides with DD-136 nematode. Plant Protection Bulletin 39:20–22.

3. Fedorko, A., M. Kamionek, J. Kozlowska, and E. Mianowska. 1977. The effects of some carbamide herbicides on nematodes from different ecological groups. Polish Ecological Studies 3:23–28.

4. Fedorko, A., M. Kamionek, J. Kozlowska, and E. Mianowska. 1977. The effects of some insecticides on nematodes of different ecological groups. Polish Ecological Studies 3:79–88.

5. Fedorko, A., M. Kamionek, J. Kozlowska, and E. Mianowska. 1977. The effect of vydate–oxamyl on nematodes of different ecological groups. Polish Ecological Studies 3:89–93.

6. Forschler, B. T., J. N. All, and W. A. Gardner. 1990. *Steinernema feltiae* activity and infectivity in response to herbicide exposure in aqueous and soil environments. Journal of Invertebrate Pathology 55: 375–379.

7. Gaugler, R., A. Bednarek, and J. F. Campbell. 1992. Ultraviolet inactivation of heterorhabditid and steinernematid nematodes. Journal of Invertebrate Pathology 59:155–160.

8. Gaugler, R., and G. M. Boush. 1978. Effects of ultraviolet radiation and sunlight on the nematode *Neoaplectana carpocapsae*. Journal of Invertebrate Pathology 32:291–296.

9. Gaugler, R., and J. F. Campbell. 1991. Behavioural response of the entomopathogenic nematodes *Steinernema carpocapsae* and *Heterorhabditis bacteriophora* to oxamyl. Annals of Applied Biology 119:131–138.

10. Hara, A. H., and H. K. Kaya. 1982. Effect of selected insecticides and nematicides on the in vitro development of the entmogenous nematode, *Neoaplectana carpocapsae*. Journal of Nematology 14:486–491.

11. Hara, A. H., and H. K. Kaya. 1983. Toxicity of selected organophosphate and carbamate pesticides to infective juveniles of the entomogenous nematode, *Neoaplectana carpocapsae* (Rhabditida: Steinernematidae). Environmental Entomology 12:496–501.

12. Hatsukade, M. 1987. Effects of entomogenous nematode, *Steinernema* spp., on the control of turfgrass insect pests. Journal of Japanese Society of Turfgrass Science 15:145–150.

13. Hatsukade, M., H. Katayama, and S. Yamanaka. 1988. Pathogenicity of the entomogenous nematode, *Steinernema* sp., to scarabaeid larvae injurious to turfgrass. Journal of Japanese Society of Turfgrass Science 17:53–58.

14. Ishibashi, N. 1992. Integrated control of insect pests by *Steinernema carpocapsae*. *In* R. A. Bedding, R.

Akhurst, and H. K. Kaya eds. Nematodes and the biological control of insect pests, 19th International Congress of Entomology, Beijing, in press.

15. Ishibashi, N., and D. R. Choi. 1991. Biological control of soil pests by mixed application of entomopathogenic and fungivorous nematodes. Journal of Nematology 23:175–181.

16. Ishibashi, N., D. R. Choi, and E. Kondo. 1987. Integrated control of insects/nematodes by mixing application of steinernematid nematodes and chemicals. Journal of Nematology 19:531 (Abstr.).

17. Ishibashi, N., and E. Kondo. 1986. A possible quiescence of the applied entomogenous nematode, *Steinernema feltiae*, in soil. Japanese Journal of Nematology 16:66–67.

18. Ishibashi, N., and E. Kondo. 1990. Behavior of infective juveniles. Pp. 139–150 *in* R. Gaugler and H. K. Kaya, eds. Entomopathogenic nematodes in biological control. Boca Raton, FL: CRC Press.

19. Ishibashi, Y., and N. Ishibashi. 1985. Bioassays of the nematicides MK-166 and oxamyl in the root-knot nematode, *Meloidogyne incognita*. Proceedings of the Association for Plant Protection of Kyushu 31: 183–185.

20. Kaya, H. K. 1985. Entomogenous nematodes for insect control in IPM system. Pp. 283–302 *in* M. A. Hass and D. C. Herzog, eds. Biological control in agricultural IPM systems. New York: Academic Press.

21. Kaya, H. K., and T. M. Burlando. 1989. Infectivity of *Steinernema feltiae* in fenamiphos-treated sand. Journal of Nematology 21:434–436.

22. Kondo, E., and N. Ishibashi. 1984. Effects of aldoxycarb treatments on body shape, motility, and infectivity of 2nd stage larvae of root-knot nematode, *Meloidogyne incognita*. Japanese Journal of Nematology 14:8–14.

23. Kondo, E., S. Honda, and N. Ishibashi. 1985. Growth and propagation of entomogenous nematodes, *Steinernema* spp., on several kinds of media prepared by chicken liver and intestine. Japanese Journal of Nematology 15:1–10.

24. Kondo, E., and N. Ishibashi. 1986. Infection efficiency of *Steinernema feltiae* (DD-136) to the common cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae) on the soil. Applied Entomology and Zoology 21:561–571.

25. Kondo, E., and N. Ishibashi. 1986. Nictating behavior and infectivity of the entomogenous nematodes, *Steinernema* spp., to the larvae of common cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae), on the soil surface. Applied Entomology and Zoology 21: 553–560.

26. Kondo, E., and N. Ishibashi. 1986. Effects of soil moisture on the survival and infectivity of the entomogenous nematode, *Steinernema feltiae* (DD-136). Proceedings of the Association for Plant Protection of Kyushu 31:186–190.

27. Lewis, E. E., R. Gaugler, and R. Harrison. 1992. Entomopathogenic nematode host finding: Response to host contact cues by cruise and ambush foragers. Parasitology 105:309–315.

28. Poinar, G. O., Jr., 1986. Entomogenous nematodes. Pp. 95–121 *in* B. D. Franz, ed. Biological plant and health protection, Stuttgart: G. Fisher Verlag.

29. Prakasa Rao, P. S., P. K. Das, and G. Padhi. 1975. Note on compatibility of DD-136 (*Neoaplectana dutkyi*), an insect parasitic nematode, with some insecticides and fertilizers. Indian Journal of Agricultural Sciences 45:275–277.

30. Rovesti, L., E. W. Heinzpeter, F. Tagliente, and K. V. Deseo. 1988. Compatibility of pesticides with the entomopathogenic nematode *Heterorhabditidis bacteriophora* Poinar (Nematoda: Heterorhabditidae). Nematologica 34:462–476.

31. Rovesti, L., and K. V. Deseo. 1990. Compatibility of chemical pesticides with the entomopathogenic nematodes, *Steinernema carpocapsae* Weiser and *Steinernema feltiae* Filipjev (Nematoda: Steinernematidae). Nematologica 36:237–245.

32. Rovesti, L., and K. V. Deseo. 1991. Compatibility of pesticides with the entomopathogenic nematode, *Heterorhabditis heliothidis*. Nematologica 37:113–116.

33. Zimmerman, R. J., and W. S. Cranshow. 1990. Compatibility of three entomopathogenic nematodes (Rhabditida) in aqueous solutions of pesticides used in turfgrass maintenance. Journal of Economic Entomology 83:97–100.