

# The role of microbial populations from long-term nonfumigant nematicide-treated soils on *Heterodera schachtii* nematicide trials

Tom T. YAMASHITA\*, David R. VIGLIERCHIO and Frances FAN-KUO

Division of Nematology, University of California, Davis, CA 95616, USA

## SUMMARY

Stock cultures of *Heterodera schachtii* were treated monthly with low doses of nonfumigant nematicide (NFN) for three continuous years (stressed populations). Soils from these stressed cultures and from a wild population culture were washed and the aqueous supernatant was freed of nematodes and eggs (leachings). Following incubation of one-half of the leachings with 10 % AC Medium for 24 hours, the microbial populations were increased approximately three-thousand-fold. The other half of the leachings were kept at 5° for 24 hours. These leachings were then added to test pots inoculated with wild-type *H. schachtii* (J2) juveniles. Two days later the pots were treated with NFN once daily for three consecutive days. Extraction of nematodes two months later indicated no detectable qualitative differences between the microbial populations in NFN-stressed vs wild-stock nematode cultures. However, leachings from NFN-stressed cultures appeared to have influential factors of unknown origin. In the absence of NFN treatment, certain leaching components stimulated nematode activity. Conversely, when treated, certain leaching components appeared to have both an additive and/or synergistic reaction with the applied NFN.

## RÉSUMÉ

Rôle joué dans les essais nématicides contre *Heterodera schachtii* par les populations microbiennes des sols traités pendant de longues périodes avec un nématicide non fumigant

Des élevages de base d'*Heterodera schachtii* ont été traités tous les mois avec de faibles doses d'un nématicide non fumigant (NNF) pendant une période de trois ans (populations sensibilisées). Le sol correspondant à ces populations sensibilisées, et celui provenant d'élevages sauvages sont mis en suspension dans de l'eau; la phase liquide supérieure (ou « filtrat ») est ensuite débarrassée des nématodes et de leurs œufs. Après incubation pendant 24 heures de la moitié du filtrat, additionnée de 10 % du milieu AC, le peuplement microbien croît d'un facteur approximatif de 3 000. L'autre moitié du filtrat est laissée 24 heures à 5°. Les deux types de filtrat sont ajoutés à des pots inoculés avec des juvéniles (J2) de la souche sauvage d'*H. schachtii*. Deux jours après les pots sont traités avec un NNF une fois par jour pendant trois jours. L'extraction des nématodes après deux mois ne permet de détecter aucune différence qualitative entre les peuplements microbiens liés aux élevages des populations sensibilisées ou sauvages. Cependant les filtrats provenant des élevages sensibilisés paraissent recéler des facteurs actifs d'origine inconnue. En l'absence de traitement avec un NNF, certains composants du filtrat stimulent l'activité du nématode. Réciproquement, s'il y a traitement, certains composants du filtrat paraissent avoir une action complémentaire et/ou synergétique vis-à-vis du NNF.

An increasing concern for environmental safety has prompted extensive studies into the role played by microorganisms in pesticide decomposition (Helling, Kearney & Alexander, 1971; Harris, 1972; Laveglia & Dahm, 1977; Woodcock, 1978). This concern has grown with the increased emphasis upon soil-applied nonfumigant organophosphates and carbamates. There is a general agreement on chemical decomposition and the role of several edaphic factors on nonfumigant nematicide (NFN) degradation (Bromilow, 1973; Caro *et al.* 1973; Smelt *et al.*, 1978a, b; Bromilow *et al.*, 1980; Gorder, Dahm & Tollefson, 1982). There are, however, opposing views on the magnitude and contribution of microbial mediated NFN decomposition. For example, some studies have indicated that microorganisms play a major role in carbofuran degradation (Williams, Peppin & Brown, 1976; Felsot, Maddox & Bruce, 1981), while

others have found no correlation between carbofuran degradation and microbial enrichment of the soil (Venkateswarlu, Siddarama Gowda & Sethunathan, 1977; Ahmad, Walgenback & Sutter, 1979). Furthermore, the various NFN's appear to have different effects on the soil microorganism population (Mathur, Hamilton & Vrain, 1980). To complicate the picture, microbial populations previously observed to degrade one particular NFN, may adapt to degrade related and unrelated pesticides as well (Kaufman & Edwards, 1982).

Previous greenhouse (Yamashita, Viglierchio & Schmitt, 1986), and laboratory (Yamashita & Viglierchio, 1987a) trials indicated that species of plant-parasitic nematodes had developed increased tolerance and/or resistance to selected NFN's. The various nematode populations used in greenhouse and laboratory tests had been stressed with monthly low doses of NFN for more

\* Current address : West Hills, Star Route 400, Lost Hills, CA 93249, USA.

than three years. Casual observations, via dilution plating, had also indicated differential microbial population levels in the various NFN-stressed nematode stock cultures.

The significance of microbial-mediated NFN degradation extends to several practical considerations, one of which involves NFN persistence and, thus, the existence of selective pressures for development of NFN resistance. If long-term monthly stressing of nematode stock cultures could also condition the microbial population for an enhanced decomposition of the NFN, the application of a soil-free suspension (leaching) from these stock cultures to nematode-inoculated test pots could possibly provide a protection from subsequent NFN treatments. This phenomenon was observed in a previous study (Yamashita, Viglierchio & Schmitt, 1986). Of equal interest would be the differential effects of leachings from the various stressed nematode stock cultures. If the application of a particular NFN can alter the of leachings from various NFN-stressed cultures of *H. schachtii* in comparison to leachings taken from a nematode stock population with no previous history of NFN stressing.

## Materials and methods

Seedlings of sugarbeets (*Beta vulgaris*) were started in 12.5 cm sterilized clay pots with an autoclaved mixture of two parts river sand to one part fine white sand. Following two months' growth, all test pots were inoculated with an aliquant of 2 000 freshly-extracted J2 stages of *H. schachtii* having no previous history of NFN treatments (wild population). One week following inoculation 200 test pots were divided into five groups. Each group (40 pots) was, then, drenched with 150 ml of leachings taken from *H. schachtii* stock cultures of either a : a) wild population (W-P); b) carbofuran-stressed population (C-S-P); c) oxamyl-stressed population (Ox-S-P), d) phenamiphos-stressed population (P-S-P); e) aldicarb-stressed populations (A-S-P). Stressed populations were generated by treating an initial wildtype population (no previous history of NFN treatment) with monthly sublethal doses for over a year before use herein (for details, see Yamashita, Viglierchio & Schmitt, 1986; Viglierchio, Brown & Fan-Kuo, 1989).

Leachings were collected from stock cultures in the following manner : 16 000 cm<sup>3</sup> of soil from each stock culture was washed in 8 dm<sup>3</sup> of tap water. After five minutes, the suspension was passed through a series of sieves with pore diameters of 833 µm, 147 µm and 25 µm. The leachings were allowed to settle before siphoning off the supernatant, which was further clarified through 75 µm and 25 µm pore sieves. One-half of the clarified leachings were amended with 3.2 gr/dm<sup>3</sup> of AC Broth Medium, aerated and incubated for 24 hours at room temperature. The remaining half was stored, unamended, for 24 hours at 5°. One-half of each group

(20 pots) was drenched with amended leachings; the remaining 20 test received unamended leachings.

Two days after the addition of leachings, test pots were treated for three successive days with either water (control) or subnematicidal levels (NFN<sub>s</sub>) for unamended leachings and a ten-fold higher concentration (NFN<sub>n</sub>) for amended leachings. The following NFN concentrations were used for treatments : carbofuran and oxamyl (NFN<sub>s</sub> = 0.008 mM, NFN<sub>n</sub> = 0.08 mM); phenamiphos and aldicarb (NFN<sub>s</sub> = 0.0012 µM, NFN<sub>n</sub> = 0.012 mM). The methods of treatment were as outlined in an earlier study (Yamashita, Viglierchio & Schmitt, 1986).

An additional group of pots, which had been drenched with amended leachings, were treated with nematicidal concentrations of NFN's made up in 50 mM phosphate buffer, adjusted to pH 6.0. During incubation of leachings with AC Medium, microbial populations generated ammoniacal odors. The use of the acidic phosphate buffer was an attempt to prevent or minimize spontaneous chemical breakdown of NFN's, which might have been mediated by an increase in pH.

Two months following treatment, all pots were harvested. Sand and roots were washed three times successively and the suspension passed through an 833 µm and onto a 246 µm pore sieve. In addition, roots were gently cleaned under a gentle stream of water (over the 246 µm sieve) to catch dislodged cysts and white females. All cysts and white females, caught on the 246 µm sieve, were later dried on filter paper then counted. Fibrous, nonstorage roots were blotted dry and the weights recorded. Populations were evaluated following a Log<sub>10</sub> (cysts + white females/gr root) transformation, where each treatment had four replicates. ANOVA was conducted using a three-factor univariate analysis. Duncan's Multiple Range Test was used for mean comparisons with an upper significance level of 5 %.

## Results

There were no appreciable differences observed at a significance level of 5 % (Tab. 2). The influence of nematicide treatments with respect to leachings (Fig. 1) and the converse effects of leachings in relation to nematicide treatments (Fig. 2) are graphically illustrated. In general, NFN<sub>s</sub> treatments on pots receiving unamended (w/o AC Medium) leachings yielded the highest population levels, mostly above the grand mean. NFN<sub>n</sub> treatments on pots with amended (w/AC Medium) leachings gave lowest nematode numbers, mostly below the grand mean. Following the partitioning of factors, it appeared that the ten-fold increase in NFN concentration was primarily responsible for this dichotomy (Tab. 1). Of the NFN treatments, oxamyl and aldicarb appeared to be the main chemicals responsible for significant population reductions (Tab. 1, Fig. 1).

Table 1

Isolated effects of different factors on *Heterodera schachtii*

A. Effects of Leachings		B. Effects of nematicides	
WILD	200 a	CONTROL	301 b
CARBOFURAN	259 a	CARBOFURAN	196 ab
OXAMYL	225 a	OXAMYL	160 a
PHENAMIPHOS	163 a	PHENAMIPHOS	255 ab
ALDICARB	213 a	ALDICARB	169 a
C. Effects of Incubating Leachings in AC Medium		D. Effects of Subnematicidal vs Nematicidal Levels of NFN	
w/o AC Medium	330 a	Subnematicidal	358 b
w/AC Medium	133 a	Nematicidal	110 a
E. Effects of Acidified Buffer			
w/o Buffer	123 a		
w/Buffer	142 a		

Numbers represent the mean populations of (cysts + white females/gram of root) for the respective variables. Those not followed by a common letter are different at a significance level of 5 % or less.

Leachings, AC Medium and acidified buffer did not appreciably affect the population levels (Tab. 1, A, C, E). For example, all test pots which were drenched in amended or unamended leachings or left untreated (controls) were statistically similar (Tab. 2). Furthermore, when unamended and amended controls were compared (e.g., WILD w/o AC Medium vs WILD w/AC Medium) it was apparent that the incubation of leachings with AC Medium and concomitant increases in microbial populations had no marked effect on nematode population levels (Tab. 2).

## LEACHINGS WITHOUT AC MEDIUM

Trends which may have practical importance are depicted in Figures 1 and 2. Untreated (control) pots, receiving leachings from carbofuran, oxamyl and phenamiphos stock cultures tended towards generally high population levels, while untreated pots drenched with wild and aldicarb stock culture leachings produced the lowest nematode numbers (Figs 1, 2). Of every leaching without AC, except for oxamyl, subnematicidal carbofuran ( $C_n$ ) treatments yielded either the highest or second to highest populations (Fig. 1). It appeared as though some form of synergistic activity between the oxamyl leachings and  $C_n$  treatment had occurred. Pots drenched with leachings from oxamyl stock cultures produced the largest number of nematodes except when treated with carbofuran, which gave the lowest number. In a similar manner, pots that had received leachings from C-S-P

stock cultures gave consistently high nematode numbers except when treated with aldicarb. Conversely, pots which had been drenched with leachings from A-S-P stock cultures tended to have low numbers (Fig. 2, subnematicidal series A).

## LEACHINGS WITH AC MEDIUM

Untreated pots previously drenched with leachings from C-S-P and A-S-P cultures yielded the highest nematode numbers (Fig. 2 w/AC Medium, B). While the leachings from C-S-P were consistent with the results without AC, the leachings from A-S-P were a complete reversal from results without AC Medium. Furthermore, incubating leachings from Ox-S-P and P-S-P stock cultures allowed for the development of some factor(s) that reduced nematode population levels (Fig. 2 B), in contrast to the effects obtained in pots without AC Medium (Fig. 2 A).

Pots receiving amended leachings from the W-P stock cultures appeared unaffected by all NFN<sub>n</sub> treatments (Tab. 2, WILD w/AC Medium). However, pots drenched with amended leachings from all stressed population stock cultures were significantly reduced in nematode numbers by one or more NFN<sub>n</sub> treatments (Tab. 2, w/AC Medium series) : a) carbofuran w/AC; CTL = 446 vs  $C_n$  = 104,  $C_n$  + Buffer = 90 and  $Ox_n$  = 98, b) oxamyl w/AC; CTL = 215 vs  $C_n$  = 33, c) phenamiphos w/AC; CTL = 230 vs  $A_n$  = 36 and  $Ox_n$  = 56 (7 % level), d) aldicarb w/AC; CTL = 516 vs  $Ox_n$  = 83.

## Discussion

Preliminary casual observations (dilution plating), indicating a several-fold greater microbial population in stressed than in wild population stock cultures, were consistent with results of field applications of NFN's on the microbial populations (Mathur, Hamilton & Vrain, 1980). The amendment of a 10 % AC Broth (designed for culturing aerobic microorganisms) to leachings, though in part arbitrary, was intended to provide a moderate enhancement of the aerobic segment of the microbial population. Following the 24 hour incubation of leachings with AC Medium, dilution plating indicated an approximate three-thousand-fold increase in the microbial population, largely represented by various species of bacteria and very few fungi.

There was an absence of significant differences either within or between control pots drenched in leachings with or without AC Medium. Microbial numbers and effects of leachings, AC Medium and buffer exhibited a negligible impact on nematode populations; however, nematicidal concentrations proved significant. The interactions between leaching, AC Medium and nematicide reveal possible trends towards certain unique qualities in the various leachings.

Table 2  
Microbial population effects on control of *Heterodera schachtii* with nonfumigant nematicides

Leachings	Nematicide Treatment				
	Control	Carbofuran	Oxamyl	Phenamiphos	Aldicarb
WILD w/o AC Medium	170 cdefghijk	442 hijk	299 defghijk	303 defghijk	233 cdefghijk
CARBOFURAN w/o AC Medium	493 ijk	514 jk	415 ghijk	603 k	212 cdefghijk
OXAMYL w/o AC Medium	532 jk	299 defghijk	545 jk	646 k	401 ghijk
PHENAMIPHOS w/o AC Medium	461 ijk	389 fghijk	191 cdefghijk	229 cdefghijk	368 efghijk
ALDICARB w/o AC Medium	156 cdefghijk	330 defghijk	253 defghijk	182 cdefghijk	289 defghijk
WILD w/AC Medium	167 cdefghijk *180 cdefghijk	173 cdefghijk	93 abcdef	298 defghijk	88 abcde
CARBOFURAN w/AC Medium	446 hijk	104 abcdefgh *90 abcde	98 abcdefg	165 cdefghijk	132 abcdefghij
OXAMYL w/AC Medium	215 cdefghijk	33 a	80 abcd *169 cdefghijk	201 cdefghijk	128 abcdefghij
PHENAMIPHOS w/AC Medium	230 cdefghijk	88 abcde	55 abc	117 abcdefghi *134 bcdefghij	36 ab
ALDICARB w/AC Medium	516 jk	186 cdefghijk	83 abcd	205 cdefghijk	176 cdefghijk *155 cdefghijk

Numbers represent the mean population of (cysts + white females/gram of root). w/AC Medium = leachings incubated following addition of 3.2 gr/L AC Broth Medium (Difco Laboratories, Detroit, Michigan) for 24 hours prior to drenching of test pots. Pots which received leachings w/o AC Medium were treated with a subnematicidal concentration of nonfumigant nematicide. Pots which received leachings w/AC Medium were treated with a ten-fold higher concentration of nonfumigant nematicide, (\*) = the nonfumigant nematicide was applied in a 50 mM phosphate buffer, pH = 6.0. Numbers not followed by a common letter are different at a significance level of 5 % or less.

Pots drenched with wild population leachings without AC Medium appeared unaffected by all NFN and control treatments. Yet, with every series of amended leachings from NFN-stressed population stock cultures, at least one or more NFN treatments resulted in a significant difference. In all cases, this difference was a population decrease, instead of the expected increase from protection by the microbial enrichment of the soil. Three observations suggest a possible explanation : a) absence of leaching effects within the controls, b) absence of NFN treatment effects in all pots drenched with wild population leachings with AC Medium, c) significant population reductions from NFN treatment to pots drenched with leachings from NFN-stressed population stock cultures. If carbofuran and its breakdown constituents were present in leachings, application of this NFN would augment control,

an effect observed with amended leachings from the C-S-P and C<sub>n</sub> treatments. An alternative explanation involves a synergistic effect whereby a chemical moiety, possibly from pesticide degradation, enhances an applied NFN effect as illustrated with enhanced N-methyl carbamate control of the green rice leafhopper (Yamamoto, Takahashi & Kyomura, 1983). Related effects have been observed with mixtures of organophosphates and carbamates (or vice versa) for enhanced control of insect populations (Ozaki, 1983). Neither can it be excluded that elevated concentrations of degradation products added with the leachings inhibited the forward reaction leading to degradation; thereby, allowing a longer period of higher nematicide concentrations to act on the nematodes.

From an earlier test in which pots of *Meloidogyne incognita* and *Xiphinema index* were drenched in

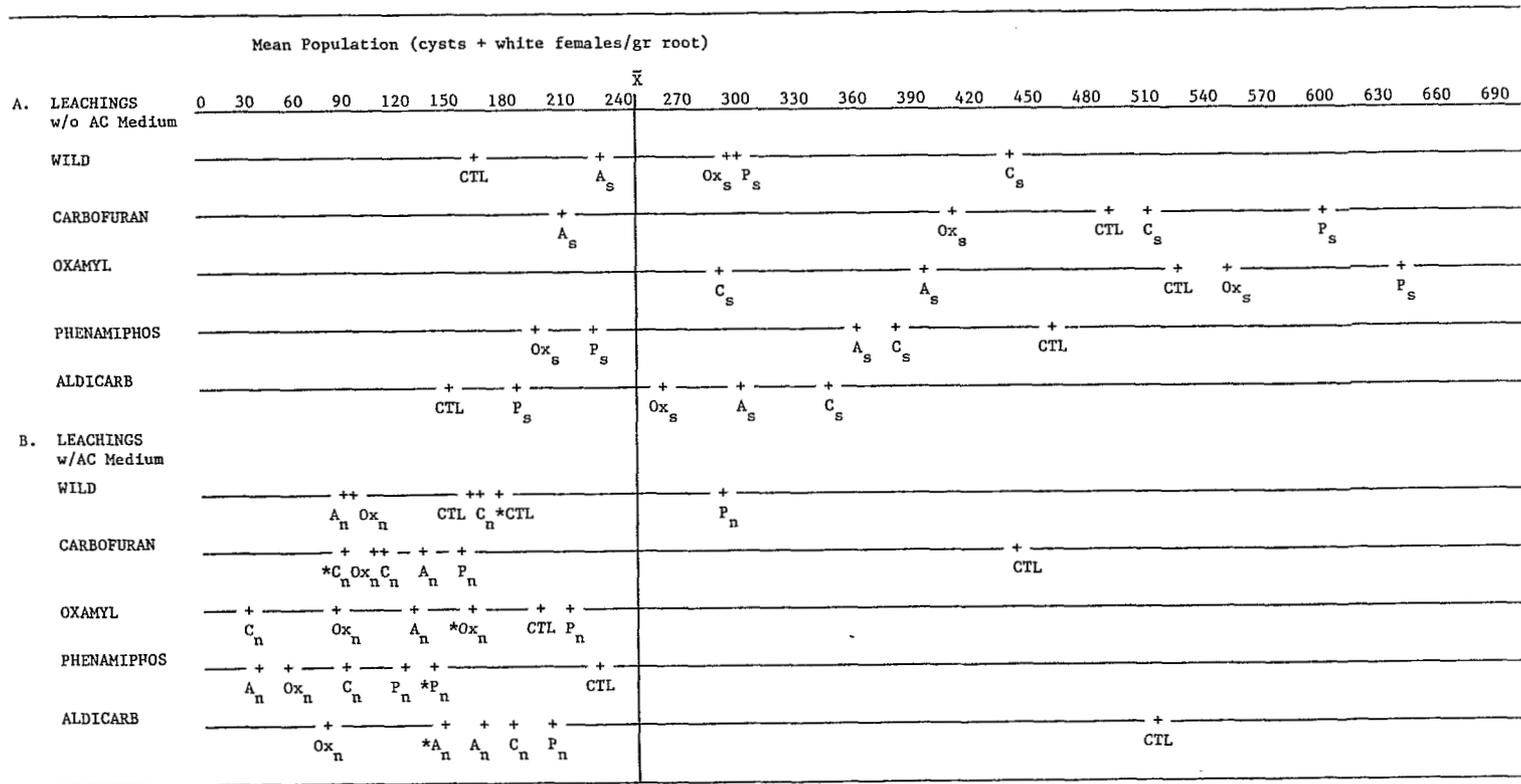


Fig. 1. *Heterodera schachtii* population levels of leachings as modified by treatments.

Leachings in (B) were incubated for 24 hours following the addition of 3.2 gr/L AC Broth Medium (Difco Laboratories, Detroit, Michigan) prior to drenching the test pots. Test pots receiving leachings without AC Medium were treated with subnematicidal levels, while those receiving leachings with AC Medium were treated with a ten-fold higher concentration of nonfumigant nematicide. Treatments are abbreviated as follows : CTL = Control, C = Carbofuran, Ox = Oxamyl, P = Phenamiphos, A = Aldicarb, subscript s = subnematicidal, subscript n = nematicidal or 10 x concentration of s. (\*) = nonfumigant nematicide applied in 509 mM phosphate buffer, pH = 6.0.

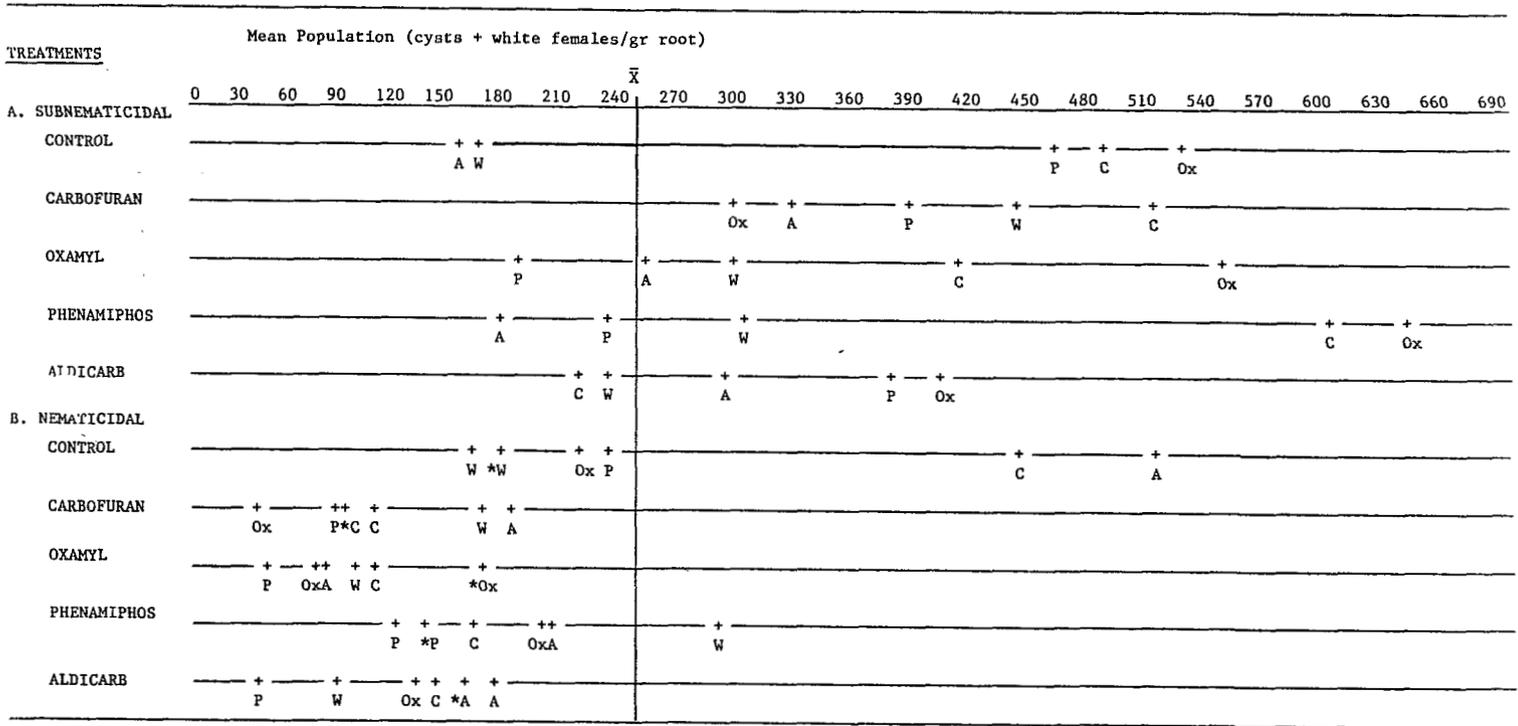


Fig. 2. *Heterodera schachtii* population levels of treatments as modified by leachings.

Leachings in (B) were incubated for 24 hours following the addition of 3.2 gr/L AC Broth Medium (Difco Laboratories, Detroit, Michigan) prior to drenching the test pots. Test pots receiving leachings without AC Medium were treated with subnematocidal levels, while those receiving leachings with AC Medium were treated with a ten-fold higher concentration of nonfumigant nematicide. Leachings are abbreviated as follows : W = Wild Populations, C = Carbofuran-Stressed Population, Ox = Oxamyl-Stressed Population, P = Phenamiphos-Stressed Population, A = Aldicarb-Stressed Population. (\*) = nonfumigant nematicide applied in 50 mM phosphate buffer, pH = 6.0.

leachings taken from NFN-stressed population stock cultures (Yamashita, Viglierchio & Schmitt, 1986), Ox-S-P leachings on *X. index* and Ox-S-P, C-S-P and P-S-P leachings applied to *M. incognita* pots resulted in markedly lower nematode numbers than undrenched pots following NFN treatments. However, *X. index* pots drenched in C-S-P and P-S-P leachings had higher population levels over undrenched pots following NFN treatment. The present study is consistent with a previous one (Yamashita & Viglierchio, 1986) for a stimulatory response in nematodes to subnematicidal levels of NFN. Perhaps this may be suspected in the apparent stimulatory response following drenches with C-S-P, Ox-S-P and P-S-P leachings without AC Medium (controls), i.e., low levels of NFN residues in leachings may have been complicating the response. Steele (1977) observed a stimulatory action of low aldicarb and carbofuran concentrations (ca. 1 µg/ml) on *H. schachtii* hatching because cysts, treated with otherwise suppressive concentrations but later freed of the NFN, exhibited markedly higher hatching than untreated cysts.

Depending on conditions, the half-life of many NFN's have been reported to range from 2-50 weeks (Getzin, 1973; Smelt *et al.*, 1978a, b; Johnson *et al.* 1981; Smelt, 1983). NFN persistence within the soil of stressed stock cultures could have been possible because they were treated one month prior to extraction of leachings (carbofuran and oxamyl applied at 1.84 µg/ml; phenamiphos and aldicarb applied at 0.23 µg/ml).

Because  $J_2$  were allowed to establish for over a week prior to leaching and NFN applications, the differential systemic capacities of the NFN's and of the different breakdown constituents may have additional bearing in this experiment. Moreover, the specific physiological changes in the plant associated with NFN applications (Milne, Van Lelyveld & Villiers, 1977; Steifert & Davidek, 1978; Sarah, 1981) may be factors in relation to altered biochemical mechanisms of plant resistance to nematodes (Giebel, 1979) that was complexed further by the specific leaching nematicide-nematicide level-AC Medium interactions leading to reduced nematode populations.

### Conclusive statements

Based upon the conditions under which this test was conducted, several conclusions can be drawn : a) the soil microbial population from stock cultures of *H. schachtii*, whether treated monthly with NFN or left untreated, appeared similar with respect to qualities of microbial-mediated protection of nematodes from NFN's, b) an approximate three-thousand-fold increase in the microorganism population had negligible effects on microbial-mediated protection from NFN's, c) possible pH-induced degradation of NFN's from ammonia-like substance in AC Medium-incubated leachings appeared

insignificant, d) certain factors in stock culture leachings appeared to react synergistically with nematicidal levels of certain NFN's for enhanced control of nematodes, e) certain factors in stock culture leachings appeared to induce stimulatory-like responses in nematodes, f) incubation of certain leachings for 24 hours in 10 % AC Medium appeared to reveal components which were manifested by an increase or decrease in corresponding control populations, g) at concentrations used, oxamyl and aldicarb, with relatively higher systemic activity, appeared to provide better control than did carbofuran or phenamiphos.

The observations of NFN resistance, indifference, habituation and increased susceptibility in greenhouse (Yamashita, Viglierchio & Schmitt, 1986), laboratory (Yamashita & Viglierchio, 1987a) and field studies (Yamashita & Viglierchio, 1987b) in various nematode species have prompted a major concern for the contribution of microbial-mediated NFN degradation. This latter phenomenon, which has been correlated often with a soil's previous history of NFN treatments, implicated microbial enrichment. However, for *H. schachtii* and based on the criterion of cysts + white females/gr root, there were no detectable qualitative differences in the soil microbial populations of monthly NFN-stressed cultures and cultures which had never been treated with NFN's. These observations merit confirmation with other nematodes in different environments and in field trials of field soil microbial populations with histories of NFN treatments.

### ACKNOWLEDGEMENTS

The authors would like to thank the Western Regional IPM Project (W-161) for their partial support of this project. We would also like to extend a special thanks to Mr. Bangtai Xu for all of his invaluable assistance in this project.

### REFERENCES

- AHMAD, N., WALGENBACH, D. D. & SUTTER, G. R. (1979). Degradation rates of technical carbofuran and a granular formulation in four soils with known insecticide use history. *Bull. environm. Contamin. & Toxicol.*, 23 : 572-574.
- BROMILOW, R. H. (1973). Breakdown and fate of oximecarbamate nematicides in crops and soils. *Ann. appl. Biol.*, 75 : 473-379.
- BROMILOW, R. H., BAKER, R. J., FREEMAN, M. A. H. & GOROG, K. (1980). The degradation of aldicarb and oxamyl in soil. *Pesticide Sci.*, 11 : 371-378.
- CARO, J. H., FREEMAN, H. P., GLOTFELTY, D. E., TURNER, B. C. & EDWARDS, W. M. (1973). Dissipation of soil-incorporated carbofuran in the field. *J. agric. & Food Chem.*, 21 : 1010-1015.
- FELSOT, A., MADDOX, J. V. & BRUCE, W. (1981). Enhanced microbial degradation of carbofuran in soils with histories of Furadan use. *Bull. environm. Contamin. & Toxicol.*, 26 : 781-788.

- GETZIN, L. W. (1973). Persistence and degradation of carbofuran in soil. *Environm. Ent.*, 2 : 461-467.
- GIEBEL, J. (1979). [Biochemical mechanisms of plant resistance to nematodes.] *Prace Nauk, Instyt. Ochrony Roslin, Poznan*, 21 : 189-212.
- GORDER, G. W., DAHM, P. A. & TOLLEFSON, J. J. (1982). Carbofuran persistence in cornfield soils. *J. econ. Ent.*, 75 : 637-642.
- HARRIS, C. R. (1972). Factors influencing the effectiveness of soil insecticides. *A. Rev. Ent.*, 17 : 177-198.
- HELLING, C. S., KEARNEY, P. C. & ALEXANDER, M. (1971). Behavior of pesticides in soils. In : Brady, N. C. (Ed.). *Advances in Agronomy. Vol. 23*, New York, Academic Press : 147-240.
- JOHNSON, A. W., ROHDE, W. A., DOWLER, C. C., GLAZE, N. C. & WRIGHT, W. C. (1981). Influence of water and soil temperature on the concentration and efficacy of phenamiphos or control of root-knot nematodes. *J. Nematol.*, 13 : 148-153.
- KAUFMAN, D. D. & EDWARDS, D. F. (1982). Pesticide/microbe interaction effects on persistence of pesticides in soil. *Comm. Vth Intern. Congr. Pesticide Chemistry (IUPAC)*, Aug. 29-Sept. 4, 1982, Kyoto, Japan.
- LEVEGLIA, J. & DAHM, P. A. (1977). Degradation of organophosphorous and carbamate insecticides in the soil and by soil microorganisms. *A. Rev. Ent.*, 22 : 403-503.
- MATHUR, S. P., HAMILTON, H. A. & VRAIN, T. C. (1980). Influence of some field-applied nematicides on microflora and mineral nutrients in an organic soil. *J. environm. Sci. & Health*, 15 : 61-76.
- MILNE, D. L., VANLELYVELD, L. J., VILLIERS, E. A. (1977). The response of peroxidase and indoleacetic acid oxidase in pineapple roots to foliar application of phenamiphos. *Agrochemophysica*, 9 : 65-69.
- OZAKI, K. (1983). Suppression of resistance through synergistic combinations with emphasis on planthoppers and leafhoppers infesting rice in Japan. In : Georghiou, G. P. & Saito, T. (Eds). *Pest Resistance to Pesticides*, New York, Plenum Press : 595-613.
- SARAH, J. L. (1981). Utilisation de nématicides endotherapiques dans la lutte contre *Pratylenchus brachyurus* (Godfrey) (Nematoda, Pratylenchidae) en culture d'ananas. III-Effets secondaires d'applications foliaires sur la réponse au traitement d'induction florale et sur la floraison. *Fruits* 35 : 491-500.
- SMELT, A. E. (1983). Effects of selected nematicides on hatching of *Heterodera schachtii*. *J. Nematol.*, 15 : 467-473.
- SMELT, J. H., LEISTRA, M., HOUX, N. W. H. & DEKKER, A. (1978a). Conversion rates of aldicarb and its oxidation products in soils. II. Aldicarb sulphoxide. *Pesticide Sci.*, 9 : 286-292.
- SMELT, J. H., LEISTRA, M., HOUX, N. W. H. & DEKKER, A. (1978b). Conversion rates of aldicarb and its oxidation products in soils. III. Aldicarb. *Pesticide Sci.*, 9 : 293-300.
- STEELE, A. E. (1977). Effects of selected carbamate and organophosphate nematicides on hatching and emergence of *Heterodera schachtii*. *J. Nematol.*, 9 : 149-154.
- STEIFERT, J. & DAVIDEK, J. (1978). The carbamoylation and spontaneous reactivation of the cabbage carboxylesterase after interaction with carbofuran. *Pesticide Biochem. Physiol.*, 8 : 10-14.
- VENKATESWARLU, K., SIDDARAMA GOWDA, T. K. & SETHUNATHAN, N. (1977). Persistence and biodegradation of carbofuran in flooded soils. *J. agric. & Food Chem.*, 25 : 533-536.
- VIGLIERCHIO, D. R., BROWN, S. M., & FAN-KUO, F. F. (1989). Adaptive responses of *Heterodera schachtii* populations to nematicidal applications of nonfumigant nematicides after stressing with sublethal doses. *Revue Nématol.* 12 (in press).
- WILLIAMS, I. H., PEPIN, H. S. & BROWN, M. J. (1976). Degradation of carbofuran by soil microorganisms. *Bull. environm. Toxicol.*, 15 : 244-249.
- WOODCOCK, D. (1978). Microbial degradation of fungicides, fumigants and nematicides. In Hall, I. R. & WRIGHT, S. J. L. (Eds). *Pesticides Microbiology, Microbial Aspects of Pesticide Behavior in the Environment*. New York, Academic Press : 731-780.
- YAMAMOTO, I., TAKAHASHI, Y. & KYOMURA, N. (1983). Suppression of altered acetylcholinesterase of the green rice leafhopper by N-propyl and N-methyl carbamate combinations. In Georghiou, G. P. & SAITO, T. (Eds), *Pest Resistance to Pesticides*. New York; Plenum Press : 479-594.
- YAMASHITA, T. T. & VIGLIERCHIO, D. R. (1986). Variations in the stability of behavioral changes in nonfumigant nematicide-stressed populations of *Xiphinema index* following release from subnematicidal stress. *Revue Nématol.*, 9 : 377-383.
- YAMASHITA, T. T. & VIGLIERCHIO, D. R. (1987a). In vitro testing for nonfumigant nematicide resistance in *Xiphinema index*. *Revue Nématol.*, 10 : 75-79.
- YAMASHITA, T. T. & VIGLIERCHIO, D. R. (1987b). Field resistance to nonfumigant nematicides in *Xiphinema index* and *Meloidogyne incognita*. *Revue Nématol.* 10 : 327-332.
- YAMASHITA, T. T., VIGLIERCHIO, D. R. & SCHMITT, R. V. (1986). Responses of nematodes to nematicidal applications following extended exposures to subnematicidal stress. *Revue Nématol.*, 9 : 49-60 —

Accepté pour publication le 22 septembre 1987.