Induction of short-term tolerance to nonfumigant nematicides in stressed and unstressed populations of *Xiphinema index*

Tom T. YAMASHITA and David R. VIGLIERCHIO

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

SUMMARY

Populations of *Xiphinema index* were stressed with monthly subnematicidal doses of either carbofuran, oxamyl or phenamiphos for five years (stressed populations). At the end of the third year, one half of these cultures were released from nematicide stress (unstressed populations). These were cultured in the absence of monthly stressing for two years. Then, both stressed and unstressed populations were treated with a subnematicidal level of nonfumigant nematicide (NFN). At various days following this treatment, nematodes were assessed for their tolerance to high concentrations of NFN. Results from this and a previous test with a wild population suggested that the demonstrated increase in tolerance to NFN may be operating by two separate mechanisms. One system is induced by the subnematicidal treatment. It is transitory and seems to operate in all populations. The other mechanism appears to be permanent and does not require induction. This latter system parallels resistance and operates in only certain stressed and unstressed populations of *X. index*.

RÉSUMÉ

Induction d'une tolérance à court terme aux nématicides non fumigants chez des populations sensibilisées et non sensibilisées de Xiphinema index

Des populations de *Xiphinema index* ont été sensibilisées par des applications mensuelles de doses subnématicides de carbofuran, oxamyle ou phenamiphos pendant cinq années (populations sensibilisées). A la fin de la troisième année, la moitié de ces élevages a été soustraite à l'action de ces nématicides (populations non sensibilisées) et ils ont été poursuivis pendant deux années sans application mensuelle des produits cités. Puis les populations sensibilisées et non sensibilisées ont été soumises à l'action de doses non nématicides de nématicides non fumigants (NNF). A des dates variables suivant le produit utilisé, les nématodes ont été alors testés pour leur tolérance à des concentrations fortes de NNF. Les résultats fournis par cet essai et ceux des essais antérieurs sur des populations sauvages suggèrent que l'accroissement démontré de la tolérance aux NNF peut résulter de deux mécanismes différents. L'un d'eux est induit par le traitement aux doses subnématicides; il est temporaire et paraît concerner tous les types de populations. Le second paraît être permanent et ne pas nécessiter de phase d'induction; ce dernier mécanisme ressemble à la résistance et concerne seulement certaines populations sensibilisées et non sensibilisées de *X. index*.

Experiments have been conducted with stressed, unstressed and wild populations of *Xiphinema index*, *Meloidogyne incognita* and *Pratylenchus vulnus* (Yamashita & Viglierchio, 1986*a*, 1986*b*, 1986*c*, 1987*a*; Yamashita, Viglierchio & Schmitt, 1986). A diverse range of altered behaviors were observed. These tests demonstrated the long-term effects of stressing and unstressing with nonfumigant nematicides (NFN). However, results from a previous study indicated that a subnematicidal treatment of wild populations may induce increased tolerance to subsequent nematicidal-level applications (Yamashita & Viglierchio, 1987*b*). In general this induced tolerance appeared to be a short-term effect. Normal behavior was usually resumed 45 days following induction treatment. This effect varied with the specific nematode species and NFN.

The induction of NFN tolerance was observed in wild populations. A question arose, then, as to whether stressed and unstressed populations would also manifest this short-term induction response. The following study addresses this question in stressed and unstressed populations of *X. index*.

Materials and methods

Two types of *X. index* populations were tested in these trials. One group had a five year history of continuous

monthly subnematicidal stressing with either carbofuran (C-S-P), oxamyl (Ox-S-P) or phenamiphos (Ph-S-P) (stressed populations). The other group had been stressed with subnematicidal doses of nonfumigant nematicides (NFN) for three years. At the end of the third year, however, these cultures were released from monthly NFN stress (unstressed populations). When the current tests were conducted, these cultures had been released from carbofuran (C-U-P), oxamyl (Ox-U-P) and phenamiphos (Ph-U-P) stressing for two years.

The methods used for induction testing were the same as outlined in a previous study (Yamashita & Viglierchio, 1987*b*). A four liter stock culture pot of the tested population was treated with a subnematicidal concentration of its respective NFN (for example, C-S-P and C-U-P with carbofuran). The subnematicidal NFN concentrations were as follows : carbofuran — 0.004 mM; oxamyl — 0.006 mM; phenamiphos — 0.0024 mM. At various days following this subnematicidal treatment (induction treatment) root and soil cores were removed from the stock pot. Extracted nematodes were then tested for their tolerance to three concentrations each of carbofuran, oxamyl and phenamiphos through an *in vitro* bioassay as used in previous studies (Yamashita & Viglierchio, 1986*c*, 1987*a*). Results from *in vitro* testing of the nematodes immediately before subnematicidal application provided a comparison for observing the effects of this induction treatment. The stressed populations used in these trials had received their last monthly stress treatment 35 days before this *in vitro* assessment.

Analysis of all data was conducted following a logit transformation (ln [number living + 0.5 divided by number dead + 0.5]). Duncan's Multiple Range Test was used in comparing mean differences with an upper significance level of 5 %.

Results

Xiphinema index (stressed populations)

Carbofuran induction treatment (CIT) of the carbofuran-stressed population (C-S-P)

On day 30 following the carbofuran induction treatment (CIT), the nematodes showed signs of reduced activity (control, Tab. 1). This effect was also observed

Table 1

Carbofuran induction of nematicide tolerance in a carbofuran-stressed population of *Xiphinema index* : percent activity following a 24 hour exposure to three nematicides

Nematicide treatment	*Before induction treatment*	*Days following induction treatment*			
		Day 5	*Day 15*	*Day 30*	*Day 45*
Stressed Control	99 *A*	93 *ABC*	99 *A*	82 *D*	92 *ABC*
Carbofuran :					
0.02 mM	99 *A*	95 *ABC*	99 *A*	89 *CD*	93 *ABC*
0.20 mM	98 *AB*	93 *ABC*	96 *ABC*	93 *ABC*	93 *ABC*
0.60 mM	97 *ABC*	97 *ABC*	98 *AB*	90 *C*	91 *BC*
Stressed Control	99 *a*	93 *ab*	99 *a*	82 *c*	92 *ab*
Oxamyl :					
0.06 mM	99 *a*	92 *ab*	99 *a*	93 *ab*	93 *ab*
0.30 mM	97 *ab*	93 *ab*	98 *ab*	96 *ab*	94 *ab*
0.60 mM	75 *cd*	91 *b*	99 *a*	77 *cd*	73 *d*
Stressed Control	99 α	93 αβ	99 α	82 γ	92 αβ
Phenamiphos :					
0.032 mM	93 αβ	96 αβ	98 α	89 βγ	90 β
0.096 mM	39 ε	58 δ	30 ζ	54 δ	33 εζ
0.160 mM	3 η	7 η	9 η	9 η	9 η

The stock culture pot was treated with 0.004 mM carbofuran (induction treatment). Soil and root cores were removed 5, 15, 30 and 45 days following induction treatment. Extracted nematodes were exposed to three concentrations each of carbofuran, oxamyl and phenamiphos for 24 hours and then evaluated active *vs* inactive using a touch-response method. Numbers represent the means of five replications. Means not followed by a common letter are significantly different at an α level of 5 % or less.

with a wild population of *X. index* (Yamashita & Viglierchio, 1987*b*). In this previously cited study CIT appeared to have increased tolerance to all concentrations of the three NFN. However, unlike the wild population, the carbofuran-stressed population (C-S-P) manifested increased tolerance in only the 0.60 mM oxamyl and 0.096 mM phenamiphos exposures. At the 0.096 mM phenamiphos exposures, there appeared to be an alternating between an increase and reduction in tolerance. This effect was also seen in the previously mentioned trials with the wild population. The greatest apparent difference between the C-S-P and the previously tested wild population was that CIT had relatively little effect on inducing increased tolerance in the former. The C-S-P demonstrated tolerance even before induction treatment. This correlated closely with earlier signs of resistance (Yamashita & Viglierchio, 1987*a*; Yamashita, Viglierchio & Schmitt, 1986).

Oxamyl induction treatment (OxIT) of the oxamyl-stressed population (Ox-S-P)

A unique effect was observed with oxamyl induction treatment (OxIT) of the Ox-S-P that was not observed with the wild population (Tab. 2). Whereas the wild population showed an immediate increase in tolerance on day 5, the Ox-S-P generally demonstrated reduced tolerance. This effect was transitory, however, as the Ox-S-P appeared to regain tolerance on days 15 through 45. In two instances the nematodes seemed to have developed higher tolerance to oxamyl (0.30 mM and 0.60 mM oxamyl on day 45). Again, at 0.096 mM phenamiphos, the nematodes alternated between increased and reduced tolerance. This effect was also observed with the C-S-P and wild populations. A major difference from the wild population, however, appeared to be a generally reduced manifestation of an induction effect in the Ox-S-P. When OxIT appeared to increase tolerance, it was primarily limited to the higher concentration exposures. That is, the supplementing effect of induction on increasing tolerance was only demonstrated in a resistant Ox-S-P at the extreme chemical exposures. The physiological processes alone, conferring nematicide resistance in the Ox-S-P, likewise expressed a degree of tolerance to the lower nematicide exposures, which was reflected in the relatively high activity percentages seen even before induction treatment.

Table 2

Oxamyl induction of nematicide tolerance in an oxamyl-stressed population of *Xiphinema index* : percent survival following a 24 hour exposure to three nematicides

Nematicide treatment	*Before induction treatment*	*Days following induction treatment*			
		Day 5	*Day 15*	*Day 30*	*Day 45*
Stressed Control	93 *ABCD*	82 *EF*	91 *BCD*	96 *ABC*	95 *ABC*
Carbofuran :					
0.02 mM	98 *A*	83 *EF*	90 *CD*	97 *AB*	95 *ABC*
0.20 mM	91 *BCD*	81 *EF*	87 *DE*	93 *ABCD*	90 *CD*
0.60 mM	72 *H*	61 *I*	93 *ABCD*	79 *FG*	73 *GH*
Stressed Control	93 *ab*	82 *ef*	91 *abc*	96 *a*	95 *ab*
Oxamyl :					
0.06 mM	92 *ab*	70 *g*	89 *abcde*	90 *abcd*	94 *ab*
0.30 mM	81 *f*	64 *gh*	84 *cdef*	94 *ab*	91 *abc*
0.60 mM	42 *i*	48 *i*	58 *h*	88 *bcdef*	83 *def*
Stressed Control	93 αβ	82 δ	91 αβγ	96 α	95 α
Phenamiphos :					
0.032 mM	98 α	85 γδ	87 βγδ	91 αβγ	92 αβγ
0.096 mM	43 ζ	25 θ	52 ε	27 θ	36 η
0.160 mM	3 τ	4 τ	9 τ	8 τ	7 τ

The stock culture pot was treated with 0.006 mM oxamyl (induction treatment). Soil and root cores were removed 5, 15, 30 and 45 days following induction treatment. Extracted nematodes were exposed to three concentrations each of carbofuran, oxamyl and phenamiphos for 24 hours and then evaluated for active *vs* inactive using a touch-response method. Numbers represent the means of five replications. Means not followed by a common letter are significantly different at an α level of 5 % or less.

Phenamiphos induction treatment (PhIT) of the phenamiphos-stressed population (Ph-S-P)

The phenamiphos induction treatment (PhIT) appeared to have affected the viability of the Ph-S-P (stressed control treatment, days 15 and 30; Tab. 3). A similar effect was observed in an earlier test with the wild population (Yamashita & Viglierchio, 1987*b*). As with the C-S-P, PhIT seemed to have had little effect on the behavior of the Ph-S-P at the lowest exposures. However, an observed effect of PhIT was an alternating between increased and reduced tolerance. For example, there was a decrease in activity percentage on day 15, when the nematodes were exposed to 0.30 mM oxamyl (63 % *vs* 81 % before PhIT). Yet, on day 5 (93 %) and day 30 (92 %) the nematodes displayed increased tolerance. This alternating effect of PhIT was also observed in earlier tests with the wild population. A concentration-dependence of the PhIT alternating effect was most evident in the phenamiphos treatments. For example, at 0.032 mM phenamiphos, there were reductions in activity percentages on days 5, 15 and 30, whereas at 0.160 mM the nematodes demonstrated increased tolerance on days 5 and 15 (in comparison to pre-induction survival). This trend of concentration-dependent variation was also seen in similar exposures of a wild population previously induced with phenamiphos.

XIPHINEMA INDEX (UNSTRESSED POPULATIONS)

Carbofuran induction treatment (CIT) of the carbofuran-unstressed population (C-U-P)

There were isolated indications of increased tolerance to 0.60 mM oxamyl on day 15 (100 %) and 0.160 mM phenamiphos on day 5 (32 %; Tab. 4). Compared to a previously tested wild population, however, the general response of this C-U-P to CIT was relatively neutral. This neutral response of the C-U-P to CIT was most evident at the two lower concentrations of carbofuran and oxamyl and at 0.032 mM phenamiphos. The general reaction of the C-S-P to CIT was also found to be indifferent (Tab. 1). There was a general pattern of response in the C-U-P, however, which set it apart from the C-S-P and wild population. This was the apparent induction of heightened sensitivity to the upper concentrations of all three NFN. For example, on days 5, 30 and 45 of the 0.60 mM carbofuran exposures, lower

Table 3

Phenamiphos induction of nematicide tolerance in a phenamiphos-stressed population of *Xiphinema index* : percent activity following a 24 hour exposure to three nematicides

Nematicide treatment	*Before induction treatment*	*Days following induction treatment*			
		Day 5	*Day 15*	*Day 30*	*Day 45*
Stressed Control	98 *A*	93 *AB*	91 *B*	91 *B*	95 *AB*
Carbofuran :					
0.02 mM	98 *A*	91 *B*	92 *AB*	82 *C*	92 *AB*
0.20 mM	92 *AB*	89 *B*	77 *C*	92 *AB*	90 *B*
0.60 mM	93 *AB*	91 *B*	89 *B*	94 *AB*	92 *AB*
Stressed Control	98 *a*	93 *abcd*	91 *abcd*	91 *abcd*	95 *abc*
Oxamyl :					
0.06 mM	96 *ab*	88 *cde*	89 *bcd*	92 *abcd*	93 *abcd*
0.30 mM	81 *e*	93 *abcd*	63 *fg*	92 *abcd*	87 *de*
0.60 mM	43 *h*	64 *fg*	69 *f*	62 *fg*	58 *g*
Stressed Control	98 α	93 αβγ	91 αβγ	91 αβγ	95 αβ
Phenamiphos :					
0.032 mM	98 α	86 γ	86 γ	88 βγ	92 αβγ
0.096 mM	40 δε	38 ε	20 ζ	46 δ	41 δε
0.160 mM	1 τ	10 η	9 ηθ	5 ηθτ	3 θτ

The stock culture pot was treated with 0.0024 mM phenamiphos (induction treatment). Soil and root cores were removed 5, 15, 30 and 45 days following induction treatment. Extracted nematodes were exposed to three concentrations each of carbofuran, oxamyl and phenamiphos for 24 hours and then evaluated for active *vs* inactive using a touch-response method. Numbers represent the means of five replications. Means not followed by a common letter are significantly different at an α level of 5 % or less.

Table 4

Carbofuran induction of nematicide tolerance in a carbofuran-unstressed population of *Xiphinema index* : percent activity following a 24 hour exposure to three nematicides

Nematicide treatment	*Before induction treatment*	*Days following induction treatment*			
		Day 5	*Day 15*	*Day 30*	*Day 45*
Unstressed Control	100 *A*	99 *A*	98 *A*	94 *ABC*	96 *AB*
Carbofuran :					
0.02 mM	98 *A*	99 *A*	99 *A*	98 *A*	97 *A*
0.20 mM	98 *A*	98 *A*	99 *A*	98 *A*	90 *BCD*
0.60 mM	97 *A*	85 *D*	96 *AB*	88 *CD*	87 *D*
Unstressed Control	100 *a*	98 *ab*	98 *ab*	94 *abc*	96 *ab*
Oxamyl :					
0.06 mM	99 *ab*	97 *ab*	99 *ab*	98 *ab*	96 *ab*
0.30 mM	92 *bc*	87 *cd*	98 *ab*	97 *ab*	87 *cd*
0.60 mM	84 *d*	71 *e*	100 *a*	88 *cd*	63 *f*
Unstressed Control	100 α	98 αβ	98 αβ	94 αβ	96 αβ
Phenamiphos :					
0.032 mM	92 β	99 αβ	98 αβ	95 αβ	94 αβ
0.096 mM	63 γδ	70 γ	19 ζ	62 δ	36 ε
0.160 mM	20 ζ	32 ε	9 η	3 η	2 η

The stock culture pot was treated with 0.004 mM carbofuran (induction treatment). Soil and root cores were removed 5, 15, 30 and 45 days following induction treatment. Extracted nematodes were exposed to three concentrations each of carbofuran, oxamyl and phenamiphos for 24 hours and then evaluated for active *vs* inactive using a touch-response method. Numbers represent the means of five replications. Means not followed by a common letter are significantly different at an α level of 5 % or less.

survival percentages were observed (85 %, 88 % and 87 % *vs* 97 % before induction). There was an isolated demonstration of increased sensitivity to 0.160 mM phenamiphos in the wild population (Yamashita & Viglierchio, 1987*b*). However, signs of heightened sensitivity were generally absent in the C-S-P.

Oxamyl induction treatment (OxIT) of the oxamyl-unstressed population (Ox-U-P)

The response of the Ox-U-P to OxIT closely paralleled that of the C-U-P to CIT (Tab. 5). There was relatively little change in the sensitivity of the Ox-U-P to all concentrations of carbofuran, the two lower exposures of oxamyl and to 0.032 mM phenamiphos. Oxamyl induction treatment, however, appeared to have induced a heightened sensitivity to 0.60 mM oxamyl and to 0.096 mM and 0.160 mM phenamiphos. On days 15 through 45, for example, the nematode activity percentages were reduced significantly (0.60 mM oxamyl and 0.160 mM phenamiphos).

Phenamiphos induction treatment (PhIT) of the phenamiphos-unstressed population (Ph-U-P)

In all the induction trials PhIT appeared to have caused an alternating between increased and reduced sensitivity to nematicides. This effect was again observed with PhIT of the Ph-U-P (Tab. 6). At 0.60 mM carbofuran, for example, the nematodes displayed increased tolerance on day 5 (96 %), appeared normal on day 15 (72 %), and on days 30 and 45 were manifesting an heightened ability to withstand carbofuran exposures (93 % and 95 %). The overall response of the Ph-U-P to PhIT was in closer agreement with the wild population (Yamashita & Viglierchio, 1987*b*) than with the Ph-S-P (Tab. 3). For example, the signs of increased tolerance to the highest concentrations of carbofuran and oxamyl (Ph-U-P, Tab. 6) paralleled the response of the wild population. In addition, the reaction of the Ph-U-P to all phenamiphos exposures closely matched the activity of the wild population.

Discussion

The effects of induction treatments appear to vary with the specific induction nematicide-nematode-*in vitro* nematicide interaction. In previous induction trials different responses were noted between *X. index* and *P. vulnus* (Yamashita & Viglierchio, 1987*b*). The current tests further indicated that there are both distinct and

Table 5

Oxamyl induction of nematicide tolerance in an oxamyl-unstressed population of *Xiphinema index* : percent activity following a 24 hour exposure to three nematicides

Nematicide treatment	*Before induction treatment*	*Days following induction treatment*			
		Day 5	*Day 15*	*Day 30*	*Day 45*
Unstressed Control	99 *A*	88 *C*	99 *A*	93 *ABC*	94 *ABC*
Carbofuran :					
0.02 mM	99 *A*	94 *ABC*	98 *A*	93 *ABC*	94 *ABC*
0.20 mM	96 *AB*	93 *ABC*	96 *AB*	91 *BC*	94 *ABC*
0.60 mM	97 *AB*	96 *AB*	93 *ABC*	88 *C*	95 *AB*
Unstressed Control	99 *a*	88 *bc*	99 *a*	93 *abc*	94 *abc*
Oxamyl :					
0.06 mM	98 *a*	94 *abc*	98 *a*	93 *abc*	95 *ab*
0.30 mM	94 *abc*	94 *abc*	98 *a*	94 *abc*	87 *c*
0.60 mM	92 *abc*	92 *abc*	78 *d*	57 *e*	52 *e*
Unstressed Control	99 α	88 γ	99 α	93 αβγ	94 αβγ
Phenamiphos :					
0.032 mM	98 αβ	91 βγ	98 αβ	93 αβγ	94 αβγ
0.096 mM	73 δ	65 ε	76 δ	77 δ	36 ζ
0.160 mM	42 ζ	40 ζ	16 η	4 θ	5 θ

The stock culture pot was treated with 0.006 mM oxamyl (induction treatment). Soil and root cores were removed 5, 15, 30 and 45 days following induction treatment. Extracted nematodes were exposed to three concentrations each of carbofuran, oxamyl and phenamiphos for 24 hours and then evaluated active *vs* inactive using a touch-response method. Numbers represent the means of five replications. Means not followed by a common letter are significantly different at an α level of 5 % or less.

subtle differences between stressed, unstressed and wild populations within the single species, *X. index*. While the unique combination of specific interacting factors may influence the expression of one particular type of response, a general characterization of wild, stressed and unstressed populations may be possible. The degree of response to induction treatments is generally greater in the wild population of *X. index* (Yamashita & Viglierchio, 1987*b*). This is not only exemplified through survival percentage comparisons before and after induction, but in the manifestation of these differences occurring even at the lowest nematicide exposures. Both the stressed and unstressed populations do not exhibit an induction effect until they are exposed to higher concentrations of nematicide. However, in most cases, the stressed and unstressed populations demonstrate a higher initial tolerance, even before induction treatments. This greater initial tolerance may be partly responsible for the seemingly indifferent response of stressed and unstressed populations to induction, expressed at the lower concentration exposures. More importantly, what this may imply is that the stressed and unstressed populations have an increased tolerance imprinted in their system. However, it appears that increased tolerance must be induced in the wild population. The heightened survival percentages, resulting from induced tolerance, closely paralleled the initially high percentages in stressed and unstressed populations prior to induction. That is, the effects of induction may temporarily compensate for a lack of inherent resistance in the wild population.

Apparently, there may be two types of systems contributing to increased tolerance. One may be permanently imprinted into the physiology of the nematode and parallels the characteristic of resistance. The other system is temporary and may be induced by a subnematicidal exposure. It appears that the wild population can only utilize an inducible system of protection. Inherent tolerance in stressed and unstressed populations, however, may also be supplemented with an inducible mechanism. This latter effect, for example, is expressed with CIT of the C-S-P (0.60 mM oxamyl; Tab. 1).

Instituting an induction mechanism appears to have a draining effect on the energy systems of the nematode. This was exemplified with the lowered activity in control treatments following induction (for example, day

5, Tab. 2 and day 5, Tab. 5). Furthermore, in earlier trials stressed populations of *X. index* demonstrated lower reproductive potentials than the wild population (Yamashita, Viglierchio & Schmitt, 1986). When the nematodes were released from stress, however, not only was normal reproduction restored, but in one population nematode numbers were increased dramatically (Yamashita & Viglierchio, 1986*a*).

The energy draining effects of induction may partly explain how resistance was selected for in stressed populations. Nematodes placed under monthly stress treatments might be able to withstand treatments for some time by virtue of induced tolerance alone. However, the selective pressures would favor those nematodes with a more permanent or constitutive range of protective processes. This can be possible inasmuch as these nematodes would not have to draw upon a sudden redirection of energy to combat stress treatments. Rather, a more permanently imprinted tolerance would have allowed a so-called normal and viable functioning of its life processes.

Yet, in situations where a wild population is subjected to an occassional nematicide application, an induction mechanism may provide for nematode energy economy. This concept has been reviewed with respect to other organisms (Brattsten, 1979).

The PhIT effects of alternating increased and reduced tolerance is difficult to explain at this time. However, in earlier *in vitro* tests it appeared that phenamiphos affected a more complex range of physiological mechanisms in the nematode (Yamashita & Viglierchio, 1986*c*, 1987*a*). This was interpreted because of the greater degree of variation in nematode survival with changes in the concentration of phenamiphos. Sudden reductions in survival percentages appear to be related to the energy draining effects of induction. For example, the Ph-S-P demonstrated sudden reductions in tolerance to all three chemicals on day 15 (Tab. 3). This was the exact time period in which the Ph-S-P expressed reduced activity following induction (control; 98 % before induction *vs* 91 % on day 15).

Table 6

Phenamiphos induction of nematicide tolerance in a phenamiphos-unstressed population of *Xiphinema index* : percent activity following a 24 hour exposure to three nematicides

Nematicide treatment	*Before induction treatment*	*Days following induction treatment*			
		Day 5	*Day 15*	*Day 30*	*Day 45*
Unstressed Control	99 *A*	91 *BC*	88 *C*	88 *C*	98 *A*
Carbofuran :					
0.02 mM	98 *A*	94 *ABC*	91 *BC*	90 *BC*	96 *AB*
0.20 mM	98 *A*	95 *AB*	81 *D*	91 *BC*	98 *A*
0.60 mM	66 *E*	96 *AB*	72 *E*	93 *ABC*	95 *AB*
Unstressed Control	99 *a*	91 *bcd*	88 *bcd*	88 *bcd*	98 *a*
Oxamyl :					
0.06 mM	98 *a*	92 *abcd*	86 *d*	91 *bcd*	95 *ab*
0.30 mM	88 *bcd*	94 *abc*	78 *e*	92 *abcd*	87 *cd*
0.60 mM	61 *g*	93 *abcd*	62 *fg*	64 *fg*	68 *f*
Unstressed Control	99 α	91 βγ	88 γ	88 γ	98 αβ
Phenamiphos :					
0.032 mM	97 αβ	92 αβγ	86 γδ	92 αβγ	96 αβ
0.096 mM	53 ζ	57 ζ	50 ζ	80 δ	72 ε
0.160 mM	36 η	28 θ	16 τ	16 τ	21 τ

The stock culture pot was treated with 0.0024 mM phenamiphos (induction treatment). Soil and root cores were removed 5, 15, 30 and 45 days following induction treatment. Extracted nematodes were exposed to three concentrations each of carbofuran, oxamyl and phenamiphos for 24 hours and then evaluated for active *vs* inactive using a touch-response method. Numbers represent the means of five replications. Means not followed by a common letter are significantly different at an α level of 5 % or less.

Conclusive statements

Through *in vitro* bioassays, the nematicide tolerances of stressed and unstressed populations of *X. index* have been evaluated at various time periods following induction treatment. When results from these trials are compared to previous tests with a wild population, two mechanisms of increased tolerance may be inferred. One system can be induced by a subnematicidal treatment. It appears to operate in all populations and is of a transitory nature. The other mechanism appears to be permanently imprinted into the physiology of the nematode. Its operation is not necessarily generated by an induction treatment. This mechanism parallels resistance and operates only in certain stressed and unstressed populations. There appears to be an additional dimension of complexity in both mechanisms. The final expression of reduced, unaffected or increased tolerance is guided by the specific induction nematicide-nematode-in vitro nematicide interaction. In this interaction the contributing factors of the nematode not only border the species level but can range to subtle differences within species as well.

Whether these or similar mechanisms of protection from nematicides are present in other nematode species is unknown at this time. It would be unusual if such systems were specific only to *X. index*. The observation of alternations in nematode activity may be of varied origin. These factors may include, among others, experimental error, multiple site attachment in relation to internal substrate concentrations, a consequence of non-instantaneous penetrability or the development of protective mechanisms.

Further research into induction effects may provide a foundation for designing more effective nematode control programs. Moreover, induction studies may also lend themselves to probing the apparent, complex biochemistry of nematodes.

Accepté pour publication le 24 avril 1986.

ACKNOWLEDGEMENTS

The authors would like to thank the American Vineyard Foundation (San Francisco, California) and the Western Pesticide Impact Assessment Program (WPIAP) for their partial support of this project. We would also like to extend a special thank you to Kathleen Yamashita for her invaluable help in this project.

This research constitutes partial fullfillment of advanced degree requirements.

REFERENCES

BRATTSTEN, L. B. (1979). Biochemical defense mechanisms in herbivores against plant allelochemicals. In Rosenthal, G. A. & Janzen, D. H. (Eds) *Herbivores,* New York, Academic Press : 200-262.

YAMASHITA, T. T. & VIGLIERCHIO, D. R. (1986*a*). 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. (1986*b*). The behavior of nonfumigant nematicide-stressed, unstressed and wild populations of *Pratylenchus vulnus* cultured on grapevines and bean plants. *Revue Nématol.,* 9 : 267-276.

YAMASHITA, T. T. & VIGLIERCHIO, D. R. (1986*c*). In vitro testing for nonfumigant nematicide resistance in *Meloidogyne incognita* and *Pratylenchus vulnus. Revue Nématol.,* 9 : 385-390.

YAMASHITA, T. T. & VIGLIERCHIO, D. R. (1987*a*). In vitro testing for nonfumigant nematicide resistance in *Xiphinema index. Revue Nématol.,* 10 : 75-79.

YAMASHITA, T. T. & VIGLIERCHIO, D. R. (1987*b*). Induction of short-term tolerance to nonfumigant nematicides in wild populations of *Xiphinema index* and *Pratylenchus vulnus. Revue Nématol.,* 10 : 93-100.

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.