Variations in the stability of behavioral changes in nonfumigant nematicide-stressed populations of *Xiphinema index* following release from subnematicidal stress

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SUMMARY

Populations of *Xiphinema index* were stressed with monthly subnematicidal doses of nonfumigant nematicides for three years, seven months. One half of these cultures were then removed from stress for 21 months (unstressed populations). Tests on the unstressed populations revealed various characteristics such as a reversion to the wild-type, retention of altered behaviors, extreme reversals in behavior and an exceptionally large increase in untreated populations.

RÉSUMÉ

Variations dans la stabilité des modifications comportementales chez des populations de Xiphinema index *sensibilisées à des nématicides non fumigants après arrêt d'une sensibilisation à des doses non toxiques*

Des populations de *Xiphinema index* ont été sensibilisées par application mensuelle, pendant trois années et sept mois, de nématicides non fumigants à des doses non toxiques. Pour la moitié de ces élevages, cette sensibilisation a été suspendue pendant 21 mois (populations désensibilisées). Les observations effectuées sur ces populations ont mis à jour certains traits particuliers tels un retour au type sauvage, le maintien de comportements altérés, des changements complets de comportement, ainsi qu'un accroissement exceptionnel de la population non traitée.

In earlier greenhouse tests, populations of *Xiphinema index* were stressed monthly with subnematicidal concentrations of carbofuran, oxamyl and phenamiphos (Yamashita, Viglierchio & Schmitt, 1986). These populations were then tested for the presence of behavioral changes that might have been brought about by monthly stressing. Results from these experiments indicated that the populations could be altered in their responses to nematicidal-level treatments. Some of these altered behaviors included signs of resistance, increased susceptibility and changes in reproductive potentials.

These types of altered behaviors have been observed in many other organisms, the most commonly known group of which are insects (Council for Agricultural Science and Technology, 1983). Various aspects of insecticide resistance have been studied. One area has been the stability of resistance following release from insecticide pressure. With respect to the stability of these behavioral changes, various characteristics such as the persistence of resistance or a reversion to wild-type behavior have been demonstrated (Brown, 1958). The following tests were conducted to explore the stability of the altered behaviors observed in stressed populations of *X. index*.

Materials and methods

Stock cultures stressed with monthly subnematicidal applications were maintained as outlined by Yamashita, Viglierchio and Schmitt (1986). After having been stressed for three years, seven months, two of the stock culture pots from each population were removed from monthly stressing. Prior to removal from stress treatments, the stock cultures had been receiving the following monthly concentrations of nonfumigant nematicides : carbofuran at 0.002 mM; oxamyl at 0.005 mM; phenamiphos at 0.0016 mM.

Unstressing involved maintaining these cultures in the absence of monthly subnematicidal treatments. These pots were maintained in a greenhouse and irrigated through drip lines delivering three equally-spaced waterings of one-half strength Hoagland's solution per day (800 mls total). The cultures were later expanded from two to four pots per population by inoculating Carignane grape seedlings with soil plugs removed from the original stock culture pots.

After 21 months without subnematicidal stressing, the nematodes were tested for the retention of various behavioral changes, originally observed with stressed populations. The methods of testing were the same as outlined by Yamashita, Viglierchio and Schmitt (1986). Two month old Carignane grape seedlings were inoculated with an aliquant of 1 000 mixed-stage nematodes extracted from the unstressed population stock cultures. Prior to inoculation, the population structure was recorded for each population. Five replications were used in the randomized complete block design. Using the carbofuran unstressed population as an example, five replication sets (one replication set = five test pots) were inoculated with nematodes from these stock cultures. One replication set was treated with nematicidal-level carbofuran, another with nematicidal-level oxamyl and a third with nematicidal-level phenamiphos. The fourth replication set was treated with the respective subnematicidal concentration (in this case subnematicidal carbofuran). The fifth replication set went untreated, receiving only one-half strength Hoagland's solution. The same series of tests were conducted with oxamyl-unstressed and phenamiphos-unstressed populations. The wild population was tested similarly but with additional subnematicidal applications from all three chemicals (carbofuran, oxamyl and phenamiphos). Concentrations of nonfumigants were identical to those used in the experiments with the stressed populations : carbofuran-nematicidal (0.040 mM); subnematicidal (0.004 mM); oxamyl-nematicidal (0.100 mM); subnematicidal (0.010 mM); phenamiphos-nematicidal (0.016 mM); subnematicidal (0.0016 mM).

The method of applying the nematicides was the same for all pots. In test pots the inoculated nematodes were allowed to establish for one week. Then, the pots went unwatered for fourteen hours before applying the chemicals. On the first day of treatment each pot received 500 mls of nematicide (or half-strength Hoagland's solution in the controls), which was sufficient to drench to excess. These applications were repeated on day two and day three, which allowed 72 total hours of exposure to treatment before normal watering was resumed.

All test pots were harvested two months following treatment. The soil from each pot was washed three times successively, the suspension being passed through an 833 µm sieve to remove large debris. Nematodes were caught on a 75 µm sieve and collected in flasks for counting. This suspension was brought up to 250 mls and three separate aliquants of 2.5 mls each were counted for population evaluation. As with the tests on stressed nematodes, the recorded populations represent the average of three counts. Root weights, degree of galling and top appearances were also recorded for each grapevine. All population data were analyzed following a $Log_{10}\ (x + 1)$ transformation. Duncan's Multiple Range Test was used for mean comparisons with an upper significance level of 5 %.

Results

The main purpose of conducting tests with unstressed populations was to observe any persistence of behavioral changes seen earlier in stressed populations. Because of this, results of the *X. index* unstressed populations will be presented under similar headings used in the earlier publication :

1. Effects of unstressing on nematode reproduction.
2. Increased susceptibility of unstressed populations to nematicidal applications.
3. Resistance in unstressed populations as evidenced by an indifferent response to nematicidal applications.
4. Resistance in unstressed populations as evidenced by their numbers being larger than the wild population following nematicidal treatment.
5. Resistance in unstressed populations as evidenced by an apparent habituation to subnematicidal applications.

Results from previous tests on the stressed populations are presented (Tab. 1) for convenience in making comparisons with the unstressed population results (Tab. 2). To simplify reading, the following abbreviations will be used in this paper :

C-S-P = Carbofuran-Stressed Population
Ox-S-P = Oxamyl-Stressed Population
Ph-S-P = Phenamiphos-Stressed Population
C-U-P = Carbofuran-Unstressed Population
Ox-U-P = Oxamyl-Unstressed Population
Ph-U-P = Phenamiphos-Unstressed Population
W-P = Wild Population (no previous history of nematicide treatment)

Results from root and top evaluations were omitted for lack of correlations.

Effects of unstressing on nematode reproduction

The effects of stressing or unstressing on reproduction can be evaluated by comparing numbers in the control columns (Tabs 1 & 2). In stressed populations (Tab. 1) it was noticed that carbofuran (570) and phenamiphos (1 214) stressing reduced reproductive potential. Oxamyl stressing did not appear to affect reproduction, as numbers from this control population (4 068) were not significantly different from the W-P control (5 334). In the unstressed populations (Tab. 2), however, freedom from carbofuran and phenamiphos stressing (for 21 months) appears to have improved reproductive potential. Whereas C-S-P control levels were only 570, unstressing had raised C-U-P levels to 1 973. These C-U-P control levels were not significantly different from the W-P control (2 926). The most dramatic effect of unstressing occurred with the Ph-U-P. Under stressed conditions, the Ph-S-P reached a low number of 1 214, but upon removal from

Table 1

Stressed population test : mean numbers of *Xiphinema index* following control, subnematicidal and nematicidal-level treatments

X. index *population*	*Nematicide Treatment*				
	Carbofuran	*Oxamyl*	*Phenamiphos*	*Control*	*Subnematicidal*
C-S-P	800 *efgh*	626 *fgh*	320 *h*	570 *h*	574 *gh*
Ox-S-P	3 212 *ab*	2 160 *bcd*	1 196 *defg*	4 068 *ab*	3 922 *ab*
Ph-S-P	2 438 *bc*	1 460 *cde*	1 256 *cdef*	1 214 *cdef*	2 752 *bc*
Wild	900 *efgh*	1 370 *cde*	4 966 *a*	5 334 *a*	

Means not followed by a common letter are significantly different at an α level of 5 % or less. C-S-P = Carbofuran-Stressed Population; Ox-S-P = Oxamyl-Stressed Population; Ph-S-P = Phenamiphos-Stressed Population; Wild = Unstressed Control Population.

Table 2

Unstressed population test : mean numbers of *Xiphinema index* following control, subnematicidal and nematicidal-level treatments

X. index *population*	*Nematicide Treatment*				
	Carbofuran	*Oxamyl*	*Phenamiphos*	*Control*	*Subnematicidal (on unstressed)*
C-U-P	1 233 *hi*	1 047 *ij*	1 327 *ghi*	1 973 *cdefg*	2 293 *cdef*
Ox-U-P	1 480 *fghi*	800 *j*	1 800 *defgh*	3 446 *bc*	1 733 *ghi*
Ph-U-P	1 647 *efgh*	1 180 *ij*	1 260 *hi*	7 780 *a*	3 940 *b*
Wild	1 133 *ij*	1 113 *ij*	2 238 *cdef*	2 926 *bcd*	
	Subnematicidal on wild population				
Wild	2 033 *cdefg*	2 693 *bcde*	2 840 *bcde*		

Means not followed by a common letter are significantly different at an α level of 5 % or less. C-U-P = Carbofuran-Unstressed Population; Ox-U-P = Oxamyl-Unstressed Population; Ph-U-P = Phenamiphos-Unstressed Population; Wild = Unstressed Control Population.

phenamiphos stressing was able to produce as much as 7 780 nematodes per pot. This number was found to be significantly larger than the W-P, C-U-P, and Ox-U-P controls (Tab. 2).

Increased susceptibility of unstressed populations to nematicidal applications

As mentioned in an earlier paper covering test results from the stressed populations, increased susceptibility in stressed and unstressed populations can be suspected when nematicide treatment lowers their numbers below : *i)* the same nematicide treatment to the wild population *ii)* the wild population control *iii)* the respective stressed and/or unstressed population control. Based on this definition, of the three comparisons, only the first two required statistically significant differences. This is best visualized by first moving down one of the chemical treatment columns and locating a number significantly lower than the W-P response to the chemical. If such a number is found, it is then compared with the W-P control and its respective stressed or unstressed population control.

In the earlier tests (Tab. 1) stressing of *X. index* with carbofuran and oxamyl appeared to have increased susceptibility to phenamiphos treatment. This increased susceptibility was maintained in the carbofuran and phenamiphos unstressed populations. Phenamiphos treatment of the C-U-P (1 327) and Ph-U-P (1 260) decreased their levels significantly below the treated W-P (2 238) and W-P control (2 296). These phenamiphos-treated C-U-P and Ph-U-P levels are also lower than their respective controls. Although phenamiphos treatment of the Ox-U-P (1 800) does not significantly reduce that population below the treated W-P (2 238), there is a strong indication of increased susceptibility in the Ox-U-P. This is suggested because phenamiphos treatment of the W-P (2 238) was not significantly reduced below the W-P control (2 926), whereas the Ox-U-P (1 800) was reduced well below the Ox-U-P control (3 446).

Resistance in unstressed populations as evidenced by an indifferent response to nematicidal applications

An indication of resistance through an indifferent response is best visualized by first noticing if the W-P is reduced by a nematicide treatment. When this is found, one would expect that a stressed or unstressed population would be comparably reduced by the same nematicide treatment. If, however, the stressed or unstressed population is not reduced below its respective control, resistance can be inferred from this indifferent response.

With the stressed population tests (Tab. 1) carbofuran and oxamyl treatment had significantly reduced the W-P (900 with carbofuran; 1 370 with oxamyl) below the W-P control (5 334). However, the C-S-P, Ox-S-P and Ph-S-P were not comparably reduced when treated with carbofuran and oxamyl. These stressed populations displayed indifference (and thus a degree of resistance) to the two nematicides. In unstressed population tests (Tab. 2) carbofuran (1 133) and oxamyl (1 113) treatments again significantly reduced the W-P below the W-P control (2 926). However, resistance to carbofuran and oxamyl (as indicated by an indifferent response) appears to have been lost in the C-U-P, Ox-U-P and Ph-U-P, as each of the unstressed populations were also significantly reduced below their respective controls.

Resistance in unstressed populations as evidenced by their numbers being larger than the wild population following nematicidal treatment

In the stressed population tests it was noticed that both the Ox-S-P and Ph-S-P displayed resistance to carbofuran treatment. Their numbers were (Ox-S-P at 3 212; Ph-S-P at 2 438) significantly larger than the carbofuran-treated W-P (900). Based on this larger population criterion, it appears that the Ph-U-P has maintained resistance to carbofuran treatment. The population level from the Ph-U-P (1 647) was significantly larger than the wild population (1 133) following carbofuran treatment. The Ox-U-P also appears to have retained resistance to carbofuran as well. Carbofuran treatment of the Ox-U-P (1 480) yields a number that exceeds the W-P (1 133) at a significance level of 10 %.

Resistance in unstressed populations as evidenced by an apparent habituation to subnematicidal applications

At a significance level of 8 %, the Ph-S-P was shown to be increased by subnematicidal phenamiphos applications (1 214 *vs* 2 752) (Tab. 1). This effect was absent in subnematicidal applications to the C-U-P, Ox-U-P and Ph-U-P (Tab. 2). An effect that approximates habituation, however, may be indicated by sublethal treatment to the C-U-P. This was shown by the fact that the W-P was reduced with subnematicidal carbofuran (2 926 *vs* 2 033; significant at the 11 % level). The same treatment of the C-U-P, however, did not result in population reduction and in fact showned signs of causing a slight increase (1 973 *vs* 2 293).

Neither of the subnematicidal oxamyl nor phenamiphos applications appeared to affect population levels of the W-P (Tab. 2). Subnematicidal carbofuran and oxamyl also appeared to have had no effect on the C-S-P and Ox-S-P (Tab. 1). However, subnematicidal oxamyl caused a significant reduction in the Ox-U-P (3 446 *vs* 1 773), an effect quite contrary to habituation. This effect was closer to increased susceptibility, as the same subnematicidal oxamyl treatment did not affect the W-P. Secondly, while subnematicidal phenamiphos caused an increase in the Ph-S-P (Tab. 1; 1 214 *vs* 2 752), the same treatment caused a significant reduction of the Ph-U-P (Tab. 2; 7 780 *vs* 3 940). This reduction of the Ph-U-P may be considered one of increased susceptibility, although the magnitude (3 940) is just as large, if not larger than, the subnematicidal treatment of the W-P (2 840).

Discussion

Effects of unstressing on nematode reproduction

Without further testing, it is difficult to accurately assess the exact nature of observed reductions or increases in control population levels. Reduced levels observed with the C-S-P and Ph-S-P controls appeared to be true characteristics of their reproductive potential, as the population structures had changed over the two months' testing period. This observed change in population structure suggested that the nematodes were feeding. Since galls were observed on these control pot vines, as well, this assumption was believed to be correct.

With these thoughts in mind, long-term stressing may have selected for nematodes able to withstand the constant (more than 36 months) subnematicidal stressing. However, ability to withstand nematicide stress may have been favored over higher reproductive potential and general fitness. Furthermore, in a stressed population, the immediate effects of the chemicals on reproduction cannot be ignored. For example, subnematicidal levels of carbofuran were shown to reduce the fecundity of *Acrobeloides nanus* (Wasilewska, Oloffs & Webster, 1975). It appears that the heterogeneous stressed population is primarily represented by nematodes able to withstand monthly nematicide stressing. Yet, because the population is heterogeneous, removal of stress has favored those few which have a higher reproductive potential. In addition, removing the stress may have eliminated the immediate effects on reproduction and both this and the selection process factors may be responsible here. These concepts are manifested in the C-S-P and C-U-P. In a stressed state the C-S-P control levels are a mere 570. When stressing is removed for 21 months, the C-U-P control levels (1 973) are restored close to the numbers obtained from the W-P control (2 926). A similar manifestation of these concepts are seen with the Ph-S-P and Ph-U-P. In a stressed state the Ph-S-P control (1 214) remained significantly below the wild population control (5 334). When monthly stressing is removed, however, the Ph-U-P control level is not only restored but becomes significantly larger than the W-P control (7 780 *vs* 2 926). This latter case has an added complexity in that the Ph-S-P demonstrated an apparent habituation to subnematicidal levels of phenamiphos (1 214 without and 2 752 with subnematicidal phenamiphos). Because the Ph-U-P and the W-P did not show this stimulatory response to subnematicidal phenamiphos, it can be suspected that the Ph-S-P was truly different. This suggests that the Ph-S-P was represented mostly by nematodes with increased tolerance and low reproductive potential. The W-P, from which all populations were started, does, in itself, demonstrate a tolerance to the concentrations of phenamiphos used (Tabs 1 & 2). But, it appears that the W-P is made up of a balanced population of nematodes with high reproductive potential and tolerance to nematicides. The Ph-S-P consists mostly of nematodes with high nematicide tolerance, while the Ph-U-P consists mostly of nematodes with high reproductive potential. This is hinted at because of three main observations :

1. Nematicidal and subnematicidal-level applications of phenamiphos to the W-P in both tests (Tabs 1 & 2) caused no marked reduction in numbers.
2. While the nematicidal-level treatment of phenamiphos appears to have had no effect on the Ph-S-P, the subnematicidal-level application appeared to stimulate population increases.
3. Both nematicidal and subnematicidal-level treatments of phenamiphos reduced the Ph-U-P levels.

It appears that stressing and unstressing can act to shift the balances between nematodes with high and low reproductive potentials as well as with high and low nematicide tolerance. As further discussion will indicate, however, in certain cases both attributes may gain expression depending upon the applied nematicide (not necessarily the same nematicide that was used for stressing).

Increased susceptibility of unstressed populations to nematicidal applications

Based on the definition of increased susceptibility, carbofuran and oxamyl stressing had made the nematodes more susceptible to phenamiphos treatment. This character was maintained in the C-U-P and Ox-U-P and also came to expression with the Ph-U-P. Earlier, the Ph-S-P did not show increased susceptibility to phenamiphos treatment. However, as mentioned in the previous section on reproduction, the shift in the heterogeneous population structure can in part explain why the Ph-U-P has become more susceptible to phenamiphos. A point which is both interesting and encouraging for practical control programs is the *consistent result of cross-susceptibility.* That is, carbofuran and oxamyl stressing had contributed to shifting the C-S-P and Ox-S-P to ones which were more sensitive than the W-P to phenamiphos treatment. Just as encouraging is the fact that even after 21 months in the absence of stressing, cross-susceptibility was maintained in these populations.

A closely related phenomenon, negatively-correlated cross-resistance, has also been demonstrated. A DDT-resistant strain of the housefly was found to be more susceptible than a wild strain to inorganic salts of bromine (Ascher & Kocher, 1954). This can be seen with the Ox-S-P, which displayed resistance to carbofuran but increased susceptibility to phenamiphos.

Resistance in unstressed populations as evidenced by an indifferent response to nematicidal applications

Indifference to carbofuran and oxamyl treatment was seen in all three stressed populations. However, during unstressing, this expression of resistance appeared to have been lost, as all three unstressed populations are reduced significantly by carbofuran and oxamyl treatment. This loss of resistance may partly be explained by shifts in the heterogeneous population. It also implies that the general character of resistance is of rare occurrence and/or not favored in the fitness of this nematode under normal conditions. While this area needs further investigation, it is apparent that removing the three populations from stress restores wild-type behavior in response to carbofuran and oxamyl treatments.

RESISTANCE IN UNSTRESSED POPULATIONS AS EVIDENCED BY THEIR NUMBERS BEING LARGER THAN THE WILD POPULATION FOLLOWING NEMATICIDAL TREATMENT

This method of comparison is very similar to what would be done in a field situation. It relies upon the simple observation of one population being larger than the W-P following treatment. The Ox-S-P (3 212) and Ph-S-P (2 438) demonstrated this manifestation of resistance to carbofuran treatment. It was retained in the Ph-U-P (1 647) and in the Ox-U-P (1 480; at the 10 % level). Such a consistent behavior in both stressed and unstressed populations may indicate the possible retention of a genetically inherited trait.

RESISTANCE IN UNSTRESSED POPULATIONS AS EVIDENCED BY AN APPARENT HABITUATION TO SUBNEMATICIDAL APPLICATIONS

Compared to its respective control, a stimulatory response to subnematicidal phenamiphos was observed in the Ph-S-P (2 752 *vs* 1,214 for the control). However, the reverse effect was seen with the Ph-U-P (3 940 *vs* 7 780 for the control), as the subnematicidal phenamiphos treatment reduced the Ph-U-P level significantly. For two distinctly opposing effects to occur, two distinctly different populations must exist. The fact that the W-P (2 840; Tab. 2) was unaffected by the subnematicidal phenamiphos treatment lends further support to this. Signs of change in the state of a population were also observed with the C-U-P (2 293; stimulatory response to subnematicidal carbofuran) and the Ox-U-P (1 773; increased susceptibility to subnematicidal oxamyl). While the specific characterizations need to be worked out, it is apparent that this nematode species is capable of changing behavior in response to stressing and unstressing.

Conclusive statements

While some requirements for insecticide resistance call for a five to ten-fold increase in tolerance, the authors have elected to use the term resistance in relation to increased nematode population survival. As field doses of nonfumigant nematicides appear to act more on nematode behavioral disruption (Marban-Mendoza & Viglierchio, 1980*a*, 1980*b*, 1980*c*) rather than outright killing, greenhouse evaluations of the resistance phenomenon have had to rely upon comparing population numbers. Although LD_{50} and related tests may give a quantitative estimation of resistance, preliminary laboratory tests indicated that the required concentrations would demand the use of impractically high concentrations, that would very likely cause phytotoxicity in field situations. The laboratory testing of these populations are being conducted and will be reported in succeeding papers.

Demonstrations of resistance, which were retained after 21 months in the absence of stressing, were seen in oxamyl and phenamiphos-stressed and unstressed populations. These populations were resistant to carbofuran. On the other extreme, the C-S-P, Ox-S-P, C-U-P, Ox-U-P and Ph-U-P showed increased susceptibility to phenamiphos. What is apparent in almost all cases in this study are the phenomena of cross-susceptibility or cross-resistance. That is, adaptation in the population to the stressing nematicide (or to the unstressing condition) appears to be specific, since subsequent exposures to another nematicide brings forth alternate behaviors. The conditioning of populations with an organic phosphate (phenamiphos) and a carbamate (oxamyl) confers resistance to the carbamate (carbofuran). Conditioning of the populations with the carbamates (both oxamyl and carbofuran) confers increased sensitivity to the organic phosphate (phenamiphos).

A very dramatic effect which occurred with unstressing was the large population build-up in the Ph-U-P control. Since the subnematicidal concentrations used in these tests approximate concentrations experienced in the field, this latter observation does merit further practical consideration. One can envision a field treated for several years with phenamiphos and then left untreated for several months. Based upon these test results, the above situation could potentially develop severe nematode problems.

Retention of some altered behaviors observed in the stressed populations may indicate true genetic characteristics. *Xiphinema index* is known to reproduce via meiotic parthenogenesis (Dalmasso, 1975). While sexual recombination is absent, there is still opportunity for genetic variation to occur. The parent W-P of *X. index* was originally taken from a fig orchard in Fresno, California by M. W. Allen. The complete life cycle of this population was found to require about 30 days at 25° on grapevines. The 36 months of stressing and 21 months of unstressing would thus allow ample opportunity for changes to occur or to be expressed. Biotypes of *X. index* have been suspected and may be a consideration in interpreting these data (Cohn, 1975).

These tests determined that both stressed and unstressed populations can behave differently from the parent W-P. Furthermore, nematodes which were removed from stress displayed various characteristics. In some cases the populations retained both resistance and increased susceptibility. Other cases showed a reversion back to wild type, while various other responses were observed, as well. In almost all cases each type of response appeared to be controlled by the specific stressed or unstressed population - nematicide treatment interaction. Further research in the characterization of these responses is warranted and should take into consideration the multidimensional complexities of nematode - nematicide interactions.

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