Nonfumigant nematicide conditioned populations of *Criconemella xenoplax* and their responses to subsequent treatments

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SUMMARY

Stock cultures of *Criconemella xenoplax* were cultured on French Colombard grapevines. These were divided into five groups for nonfumigant nematicide (NFN) stressing. Each group received monthly low doses of either carbofuran, oxamyl, phenamiphos and aldicarb solutions or water. After more than twelve months of stressing, the five populations were tested for their response to NFN treatments. Stressed populations appeared to respond differently than the untreated population. Characteristics which surfaced were changes in reproductive potential, increased susceptibility; increased populations responded in the aforementioned manner to NFN to which they had no previous history of exposure. This latter response approximated cross-susceptibility and cross-resistance.

RÉSUMÉ

Populations de Criconemella xenoplax *sensibilisées aux nématodes non-fumigants et leurs réactions aux traitements ultérieurs*

Des élevages en masses de *Criconemella xenoplax* ont été effectués sur vigne (cépage French Colombard). Ils ont été divisés en cinq lots en vue de leur sensibilisation aux nématicides non-fumigants (NNF). Chacun de ces lots a été soumis chaque mois à des doses faibles de solution de carbofuran, d'oxamyle, de phenamiphos ou d'aldicarbe. Après plus de douze mois d'une telle sensibilisation les cinq lots ont été testés pour leur réaction aux traitements à l'aide de NNF. Les populations sensibilisées ont des réactions différentes de celles des populations témoins, non traitées. Les caractéristiques notables de ces réactions sont une modification du potentiel reproducteur et une augmentation de la sensibilité, les populations, en accroissement, répondant de cette manière aux NNF auxquels elles n'avaient pas été sensibilisées. Une telle réaction fait penser à une sensibilité et à une résistance croisées.

The ring nematode, *Criconemella xenoplax* (Raski) Luc & Raski, is a plant-parasitic species of particular importance in perennial fruit crop production. For example, it has been implicated as a major contributing factor to the peach tree short-life problem (Chitwood, 1949; Barker & Clayton, 1973; Nyczepir *et al.*, 1983). Bacterial canker, which continues to be a major disease of stonefruits (Otta & English, 1970), has been shown to be closely correlated to debilitating populations of *C. xenoplax* (Lownsbery *et al.*, 1973; Mojtahedi, Lownsbery & Moody, 1975; Lownsbery *et al.*, 1977; English *et al.*, 1983). Additionally, imbalances in plant hormones and subsequent interferences with dormancy brought about by root feeding of this nematode have contributed to cold damage (Carter, 1976). The nematode is not limited to stonefruits but has been found associated with declining walnut orchards (Lownsbery *et al.*, 1978), and the senior author has observed large populations of *C. xenoplax* in weakened vineyards and ornamental plantings.

Subsequently, marked improvements in plant growth as well as reductions in disease incidences have been demonstrated with such practices as preplant backhoeing and fumigation (English *et al.*, 1983). However, recent banning of fumigants such as DBCP and EDB have prompted an interest in nonfumigant nematicides (NFN) as viable alternatives (Raski, 1981). Oftentimes, the effective application procedures have called for repeated low doses applied at periodic intervals throughout the year. As a substitute to this procedure, a new approach focuses upon incorporating controlled release granular nematicides which deliver relatively constant doses during the granules' effective life (Boehm, 1986). Resultingly, elective pressures may contribute to the development and/or selection of tolerant or resistant strains which can nullify an investment in control programs. The reality of this phenomenon had been hinted at in earlier studies with *Paratylenchus hamatus* on greenhouse roses (MacDonald, 1976) and with *Pratylenchus scribneri* in field corn (Smolik, 1978). Recent studies have helped to verify and define the occurrence of resistance and related behavioral changes in plant-parasitic species (Yamashita & Viglierchio, 1986 *a, b, c;* 1987 *a, b, c, d;* Yamashita, Viglierchio & Schmitt, 1986).

The following study addresses questions regarding the behavior of *C. xenoplax* to control treatments following long-term, repeated exposures to low levels of four commonly used NFN.

Materials and methods

Approximately 2 000 mixed-stages of *C. xenoplax* were inoculated onto three-month-old French Colombard seedlings rooted from two-bud cuttings. Grapevines were grown in four-liter pots using a sterilized mixture of two parts river sand to one part soil. These stock cultures were allowed to establish for two months before initiating monthly low doses of NFN as outlined in a previous study (Yamashita, Viglierchio & Schmitt, 1986). The NFN and their initial concentrations were as follows : carbofuran and oxamyl (0.002 mM), phenamiphos and aldicarb (0.0002 mM). Populations were monitored periodically and when their numbers appeared to have increased, the monthly NFN doses were stepped up in concentration. At the time of testing, the populations were receiving the following monthly treatments : carbofuran and oxamyl (0.008 mM), phenamiphos and aldicarb (0.0012 mM).

Following twelve months NFN conditioning, the wild and stressed populations were tested for their response to NFN. Prior to their extraction for testing, stressed populations had received a monthly subnematicidal dose 30 days in advance. Suspensions of nematodes caught on a 74 µm sieve were further clarified through sugar flotation. Following aeration for one hour, an aliquant of 1 000 mixed-stage nematodes were inoculated onto three-month-old French Colombard seedlings. The grapevines were grown in sterilized 12.5 cm diameter clay pots in a 2 : 1 mixture of autoclaved river sand to soil. The test was conducted with four replications using a completely randomized design. After allowing the populations to establish for one week, the test pots were drenched to excess on three successive days with the following NFN : carbofuran and aldicarb (subnematicidal = 0.008 mM; nematicidal = 0.08 mM), phenamiphos (subnematicidal = 0.0012 mM; nematicidal = 0.012 mM). The methods of treatment were as outlined in a previous study (Yamashita, Viglierchio & Schmitt, 1986).

Test pot cultures were grown for two months before their populations were evaluated. Suspensions were passed through a 246 µm sieve. Nematodes caught on a 35 µm sieve were further clarified through sugar flotation. Three aliquants were counted successively and averaged for final population evaluations. Populations were analyzed following a Log_{10} (nematode population) transformation. Mean comparisons were conducted using Duncan's Multiple Range Test with an upper significance level of 5 %.

Results

Experimental results were organized and evaluated according to five principal concepts. Although some may tend to overlap, these categories remain areas of major concern and serve to facilitate an understanding of the overall complexity :

1. Effects of monthly subnematicidal stressing on nematode reproduction.
2. Increased susceptibility of stressed populations to NFN applications.
3. Resistance to NFN in stressed populations appearing as :
   a. an indifferent response to chemical treatments.
   b. a larger population level following chemical treatments.
   c. an apparent habituation to chemical treatments.

For brevity, the following abbreviations will be used :
C = carbofuran, Ox = oxamyl, P = phenamiphos, A = aldicarb; the subscript s signifies subnematicidal dose, e.g., C_s = subnematicidal carbofuran; the subscript n signifies nematicidal dose, e.g., C_n = carbofuran nematicidal dose (10 × C_s); CTL = control (no chemical treatment). Nematode populations are indicated thusly : W-P = wild population (no previous exposure to NFN); C-S-P = carbofuran stressed population and similarly for Ox-S-P, P-S-P and A-S-P.

Effects of monthly NFN stressing treatments on reproduction

They are best viewed in a comparison of numbers from the CTL column (Tab. 1). A significantly low number of nematodes recovered from the phenamiphos-stressed population (P-S-P = 59) suggested a reduction in reproductive potential from wild (W-P = 908), carbofuran (C-S-P = 3 917), oxamyl (Ox-S-P = 2 158) and aldicarb (A-S-P = 3 281) populations. However, at significance levels of 6 % and 10 %, respectively, the C-S-P and A-S-P appeared to have increased reproductive capacity above that of the W-P. There appeared to be no differences between the C-S-P, Ox-S-P and A-S-P.

Increased susceptibility of stressed populations

It can be inferred when a treated, stressed population level falls below : a) the same NFN treatment to the W-P, b) the W-P control, and c) the respective stressed population control. Populations which met this criterion were the A-S-P, treated with subnematicidal carbofuran (C_s = 235, Tab. 1) and the P-S-P, treated with nematicidal oxamyl (Ox_n — 14, Tab. 1). The effect seen with the A-S-P appeared to be inversely concentration-dependent, as the additional population reduction expected in the transition from C_s to C_n treatment was not observed.

Table 1
Response of various populations of *Criconemella xenoplax* to nonfumigant nematicides

	Nematicide treatments								
Population	*CTL*	C_s	C_n	Ox_s	Ox_n	P_s	P_n	A_s	A_n
W-P	908 defghi	1 552 fghijklm	1 202 efghijk	1 125 efghij	1 312 efghijkl	579 defg	386 def	817 defgh	356 de
C-S-P	3 917 ijklmn	8 492 n	1 626 fghijklm	3 917 ijklmn	4 178 jklmn	3 707 ijklmn	912 defghi	4 036 jklmn	4 966 klmn
Ox-S-P	2 158 ghijklm	5 248 lmn	1 211 efghijk	1 556 fgijklm	1 750 ghijklm	3 228 hijklmn	966 efghij	6 209 mn	668 defg
P-S-P	59 b	1 592 fghijklm	62 b	579 defg	14 a	76 bc	41 ab	29 ab	1 807 ghijklm
A-S-P	3 281 kijklmn	235 cd	975 efghij	1 040 efghij	769 defgh	1 297 efghijkl	685 defg	1 622 fghijklm	1 675 ghijklm

Nematicide treatments are abbreviated as follows : CTL = Control, C = Carbofuran, Ox = Oxamyl; P = Phenamiphos and A = Aldicarb; subscript s = subnematicidal and subscript n = nematicidal. Numbers not followed by a common letter are different at a significance level of 5 %. Additional designations are : W-P = Wild Population, C-S-P = Carbofuran-Stressed Population, Ox-S-P = Oxamyl-Stressed Population, P-S-P = Phenamiphos-Stressed Population and A-S-P = Aldicarb-Stressed Population.

Resistance to NFN in stressed populations

It can be manifested in three different ways :

An indifference response to chemical treatments. For example, if a chemical treatment reduces the W-P below its respective control, a comparable reduction would be expected for each stressed population. The absence of a comparable population reduction (indifference) would suggest a degree of resistance to the NFN. At the significance level of 5 % there were no reductions in the W-P with all tested NFN (Tab. 1). However, at an approximate level of 10 %, A_n reduced the W-P below the W-P control (A_n = 356 *vs* CTL = 908, Tab. 1). Comparable reductions were not observed with the C-S-P (A_n = 4 966 *vs* CTL = 3 917), P-S-P (A_n — 1 807 *vs* CTL = 59) and the A-S-P (A_n = 1 675 *vs* CTL = 3 281). Accordingly, it may be suspected that these three populations displayed a degree of tolerance to the nematicidal level of aldicarb.

Larger population levels following chemical treatments. It is a straightforward criterion. This merely requires a larger population build-up of a stressed population over that of the W-P, following NFN treatments. The C-S-P demonstrated this form of resistance to all NFN, including C_s (C-S-P = 8 492 *vs* W-P = 1 552), Ox_n (C-S-P = 4 178 *vs* W-P = 1 312), P_s (C-S-P = 3 707 *vs* W-P = 579), A_s (C-S-P = 4 036 *vs* W-P = 817) and A_n (C-S-P = 4 966 *vs* W-P = 356). The Ox-S-P responded in a similar manner to subnematicidal levels of both phenamiphos (Ox-S-P = 3 228 *vs* W-P = 579) and aldicarb (Ox-S-P = 6 209 *vs* W-P = 817). Additionally, both the P-S-P and A-S-P were able to withstand a nematicidal level aldicarb treatment better than did the W-P (P-S-P = 1 807 and A-S-P = 1 675 *vs* W-P = 356).

An apparent habituation to chemical treatments. It occurs when the nematode numbers increase following NFN treatment, as opposed to no treatment. As a consequence, the population appears to have developed a form of physiological need for the NFN. This effect was observed with the C-S-P and P-S-P (Tab. 1). When the C-S-P was left untreated, the population reached a mean level of 3 917 nematodes per test pot. Following treatment with C_s, however, the population was increased to a mean level of 8 492 nematodes per test pot. This was statistically larger at a level of 6 %. The response of the P-S-P to NFN was even more dramatic. The P-S-P control provided 59 nematodes per test pot, whereas population levels following treatments with Ox_s, C_s and A_n were increased to 579, 1 592 and 1 807 nematodes per test pot, respectively. At a significance level of 7 %, A_s applications to the Ox-S-P caused an increase in population levels (Ox-S-P, CTL = 2 158 *vs* A_s = 6 209). There were no effects of this nature seen with the A-S-P.

Discussion

Monthly subnematicidal stressing

Some effects of monthly subnematicidal stressing on nematode reproduction resulted in the low nematode levels found in the untreated as well as in many of the NFN treated P-S-P, thereby initially suggesting a stabilized and reduced reproductive capacity; however, this population may have demonstrated a condition approximating more of a " repressed " physiology and/or reproductive capacity. When treated with subnematicidal levels of both carbofuran and oxamyl or with a nematicidal level of aldicarb, the P-S-P appeared to be stimulated or induced to resume normal activity

(W-P, CTL = 908; P-S-P, CTL = 59 *vs* C_s = 1 592, Ox_s = 579, A_n = 1 807). Furthermore, when the P-S-P was treated with nematicidal levels of oxamyl, the population was reduced to even lower numbers (Ox_n = 14). The condition being used here to explain the physiological state of an untreated, stressed population, " reproductive capacity ", facilitates description of the end result and does not imply a stabilized, unwavering characteristic. Rather, the condition is more one of a highly dynamic and responsive physiological make-up, which reacts specifically to various combinations of NFN, their different concentrations and the sequence of specific NFN treatments related to a previous NFN stressing. This point was further illustrated in the opposing responses of the C-S-P and A-S-P to subnematicidal carbofuran treatments. Both the untreated C-S-P and A-S-P were found to have higher numbers than the W-P at the 6 % and 10 % significance levels, respectively. When treated with C_s, however, the population level of the C-S-P increased dramatically (C-S-P, CTL = 3 917 *vs* C_s = 8 492). Yet, the A-S-P levels were reduced considerably following C_s treatment (A-S-P, CTL = 3 281 *vs* C_s = 235). The specificity of these interactions were also observed in previous tests with *Xiphinema index* (Yamashita & Viglierchio, 1986 *b;* Yamashita, Viglierchio & Schmitt, 1986). Furthermore, the differential response of *Pratylenchus vulnus* to NFN with respect to a different host has been demonstrated (Yamashita & Viglierchio, 1986 *a*).

In a previous test NFN stressed populations of *X. index* were removed from stress for 21 months and tested for their responses to water and NFN treatments (Yamashita & Viglierchio, 1986 *b*). The P-S-P removed from stress (P-U-P) responded with a dramatic increase in population when left untreated. It appeared that stressing had selected from a heterogeneous population, nematodes with heightened ability to withstand monthly NFN stressing. However, when removed from stress and left untreated, large population increases in the P-U-P appeared to be the result of a shift in the population from nematodes with increased tolerance to NFN to nematodes with increased reproductive capacity and low NFN tolerance. This type of phenomenon appeared to have occurred in the C-S-P and A-S-P of *C. xenoplax* in response to P_n treatments. When left untreated, their numbers remained above the W-P. However, when treated with a nematicidal level of phenamiphos (P_n), they were reduced significantly, while the W-P remained relatively unaffected (W-P, CTL = 908 *vs* P_n = 386; C-S-P, CTL = 3 917 *vs* P_n = 912; A-S-P, CTL = 3 281 *vs* P_n = 685).

INCREASED SUSCEPTIBILITY OF STRESSED POPULATIONS

This was observed in the P-S-P (Ox_n) and A-S-P to treatments of P_n and C_s, respectively, which also served as examples of cross-susceptibility. In fact, neither population appeared to be affected by either a subnematicidal or nematicidal application of its respective chemical (i.e., P-S-P with P_s or P_n and A-S-P with A_s or A_n). Additionally, while one would expect a further reduction in nematode numbers following an increase in NFN dosage, this effect was not observed with the carbofuran treatments to the A-S-P. Similar effects were observed in earlier studies using an *in vitro* bioassay (Yamashita & Viglierchio, 1985 *a, b*). In these tests lower or intermediate doses of NFN appeared to express differences between populations of *X. index, Meloidogyne incognita* and *P. vulnus* better than did the highest concentrations. Conversely, stimulatory type responses to NFN treatment over nontreatment had been observed with *C. xenoplax* (e. g., C-S-P, CTL = 3 917 *vs* C_s = 8 492) and, perhaps, this phenomenon can be equated to the conditions observed in the transitions from low to higher doses of NFN previously mentioned. A higher rate of aldicarb and the lower rate of phenamiphos (Santo, Ponti & Wilson, 1983 *a*) applied for the control of *C. xenoplax* in concord grape plantings, resulted in nematode population levels greater than in the untreated plots. A similar condition was observed in a three-year study on concord grape plantings in which the upper (9.3 ℓ/ha) and lower (2.3 ℓ/ha) application rates of oxamyl resulted in numbers of *C. xenoplax* well above that of both the intermediate rate plots (4.7 ℓ/ha) and the untreated plots (Santo, Ponti & Wilson, 1983*b*).

RESISTANCE TO NFN IN STRESSED POPULATIONS

This was evidenced by :

An indifferent response to chemical treatments in which, at the 10 % level of significance, the W-P was reduced by A_n treatments. However, comparable reductions were not seen with A_n treatments to the C-S-P, P-S-P and A-S-P. An argument often raised to explain results of this nature is that the apparently resistant populations represented nematodes with improved reproductive capacity and not characteristics of increased NFN tolerance. That is, the stressed populations showing indifference were, in fact, affected equally as much as the W-P but by virtue of improved reproductive potentials were able to reestablish high numbers. If this were the case, then, one would expect a quantitative relationship between the effects of a subnematicidal dose *vs* a ten-fold increase or nematicidal dose. For example, when the Ox-S-P was treated with nematicidal aldicarb (A_n), the resulting population levels of 668 represented approximately a ten-fold decrease in the numbers resulting from subnematicidal aldicarb (A_s) treatment, 6 209. However, this was not observed with either the C-S-P or the A-S-P treated with A_s or A_n. Furthermore, the P-S-P was, in fact, significantly increased to more than 60 times the levels resulting from A_s treatment (A_s = 29 *vs* A_n = 1 807). Not only were the C-S-P, P-S-P and A-S-P more tolerant to A_n

treatments but the P-S-P actually did better following A_n applications.

Larger population levels following chemical treatment only with the nematicidal aldicarb (A_n) treatment, which was observed to reduce the W-P below the W-P control (W-P, CTL = 908 *vs* A_n = 356; 10 % level of significance). Thus, the larger population levels seen in the C-S-P (4 966), P-S-P (1 807) and A-S-P (1 675) following A_n treatment may possibly have been a result of increased tolerance and/or resistance to aldicarb. While applications of C_s, Ox_n and P_s to the C-S-P and P_s to the Ox-S-P resulted in population levels significantly above the same treatment to the W-P, it is uncertain at this time whether or not this was the result of increased tolerance and/or resistance or other characteristics. What is important, however, is that under field conditions, populations with these properties could, by virtue of their numbers, alone, cause considerably more economic damage to the crops.

All cultures of *C. xenoplax* used in these tests were originally taken from a peach orchard in Merced County, California by B. F. Lownsbery. While this original field population should have been represented by a potentially heterogeneous gene pool, the breadth of heterogeneity may have been relatively more limited by the peach host than another host such as grapevines. Moreover, strain variation within nematode species is well documented, therefore it is not surprising for stressing to have either selected and/or conditioned the original W-P to withstand and/or respond to NFN treatments with relatively larger population levels. Yet, the W-P, however heterogeneous, was incapable of demonstrating the vigorous responses indicative of the stressed populations. Long-term field studies with NFN for the control of *C. xenoplax*, however, have indicated an adaptability of the heterogeneous field population parasitizing concord grapevines (Santo, Ponti & Wilson, 1983 *a, b, c, d*). In many cases population levels from NFN-treated plots were larger and/or equal to the levels observed in untreated plots. In addition, while carbofuran conditioning resulted in a population capable of producing large numbers (present study), four years of carbofuran treatment on a concord grapevine population were shown to reduce their numbers below the untreated plots (Santo, Ponti & Wilson, 1983 *a*). A three-year field test conducted with carbofuran on peaches, however, yielded population levels comparable to trends observed in the present study (Ritchie & Bennet, 1983). It is pertinent, then, to consider not only the degree of population heterogeneity associated with particular hosts but the differential response of any one population during testing as affected by the specific host. This phenomenon was graphically illustrated in a previous study with various populations of *P. vulnus* and its expressions of various characteristics as influenced by Kentucky Wonder beans *vs* Thompson Seedless grapevines (Yamashita & Viglierchio, 1986 *a*).

An apparent habituation to chemical treatments. Some workers have attempted to explain the effects of habituation as a result of population reductions in predators and/or competitors. However, if this were true, comparable increases in nematode numbers would be observed in the W-P, and this is not seen. A second argument that has been raised is that reduced populations of predators and/or competitors in stressed stock cultures accounted for a reduced number of these factors being inoculated along with *C. xenoplax*. However, the senior author examined stock cultures and found no differences in populations of predators and/or competitors or between inoculating populations.

The stimulatory response to NFN observed in these tests approximated one of dependence or habituation. This phenomenon has been recorded in lannate-resistant mutants of *Caenorhabditis elegans* in which certain strains were observed to be dependent upon the chemical for normal activity (Brenner, 1974). During periodic monitoring of stock stressed populations of *X. index*, the senior author consistently found the highest population levels in pots treated with phenamiphos, followed by oxamyl, untreated and carbofuran. With *P. vulnus*, highest populations were extracted from pots stressed with carbofuran, followed by oxamyl, untreated and phenamiphos. Previously conducted field studies indicated that the levels of *X. index* taken from plots treated for three years with phenamiphos and carbofuran were significantly higher than numbers from the control plots (Yamashita & Viglierchio, 1985 *c*).

Furthermore, the majority of nematodes which had received a 24-hour exposure to nematicidal levels of NFN survived a 72-hour incubation in water at 25°, while most of the untreated nematodes were found dead (Yamashita & Viglierchio, 1985 *c*). It should not be surprising that the C-S-P, Ox-S-P and the P-S-P would respond in a stimulatory manner to certain NFN treatments. What is interesting is that this response oftentimes followed treatments with a NFN to which the population has never been exposed. This latter effect is of particular importance when designing control programs which incorporate the alternating of chemicals to avoid or minimize resistance factors.

Conclusive statements

Tests with various stressed populations of *C. xenoplax* have demonstrated several phenomena, the nature of which is not unlike those observed in previous tests with stressed populations of *X. index*, *M. incognita* and *P. vulnus*. The responses of five populations of *C. xenoplax* receiving nine different treatments graphically illustrate (Fig. 1) the capacity of this nematode to adapt to nematicide stress and most probably other forms of stress. With the overall grand mean of populations as a conservative frame of reference the responses to treatments of the wild and aldicarb-stressed populations cluster about the mean, whereas the phenamiphos-stressed population also cluster but below the mean. In contrast the responses of the carbofuran or oxamyl-stressed populations do not cluster but spread out above the mean. Although many other comparisons and interpretations of the results are possible, those selected herein were considered worthy of emphasis.

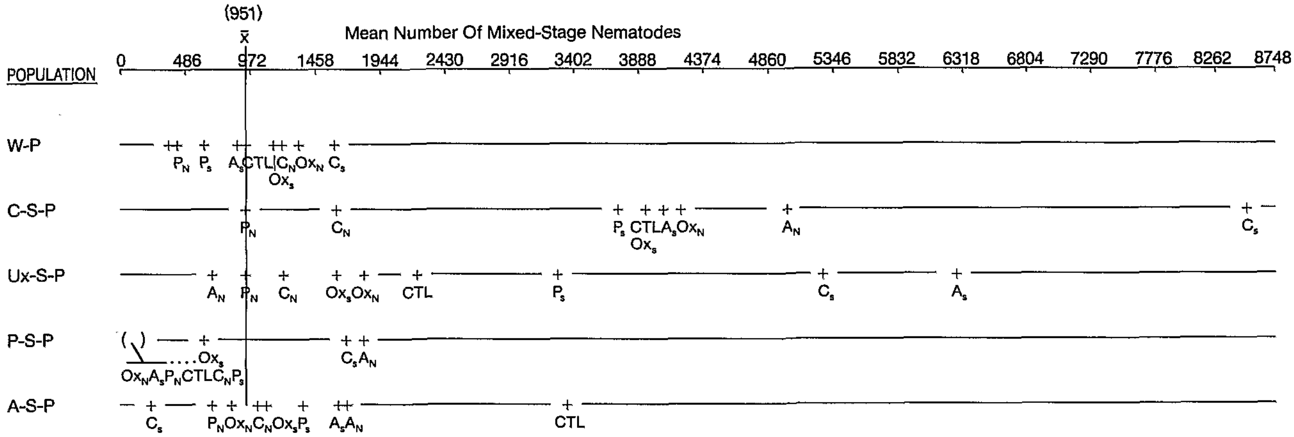

Fig. 1. Response of various populations of *Criconemella xenoplax* to nonfumigant nematicides.

Nematicide treatments are abbreviated as follows : CTL = control; C = carbofuran; OX = oxamyl; P = phenamiphos; A = aldicarb. Subscript $_n$ = nematicidal; subscript $_s$ = subnematicidal.

Nematode populations are abbreviated as follows : W-P = wild population; C-S-P = carbofuran-stressed population; OX-S-P = oxamyl-stressed population; P-S-P = phenamiphos-stressed population; A-S-P = aldicarb-stressed population.

When designing nematode control programs with fumigants, it may not have been in error to approach the task with the idea that one nematode was like another. With the advent of NFN, however, the frame of mind must change from one of generalizing to one of recognizing the specific interactions between nematode species, the NFN applied, the NFN rate and the host. It has been a major goal of the authors to conduct these tests in an effort to define the many parameters influencing control of nematodes with NFN. Hopefully, these and succeeding tests will add to the library of information needed in developing effective control strategies with the relatively new NFN.

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