

Tribune

THE IMPACT OF NEMATODE ADAPTABILITY ON THE PROSPECT FOR THEIR CONTROL

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Nature evolved a way to cope with change early in its history, perhaps even before the appearance of life forms. For drastic environmental changes, coping was equally drastic, e.g., the collapse of dinosaur dominance eventually to be replaced by that of mammals. Evolution continues to be fueled by flexibility and adaptability of species; inflexible species unable to adapt to environmental pressures of whatever origin, disappear, an observation consistent with the fossil records. This capacity to adapt is inherent in most organisms; moreover, the environmental stress driving the process is not limited to climatic or habitat modifications, but is

faithful shadow" (Katner & Ling, 1989). The widespread use of antibiotics during the last half century has dramatically raised the specter of drug resistance development to near catastrophic proportions in modern medicine. In a parallel situation the use of modern pesticides for weed, insect, and plant pathogen control resulted in dramatic increases in pest resistance to the point that hundreds of pesticides have become useless (Anon., 1986). Until recently, nematodes had been essentially ignored with respect to a general capacity to adapt to pesticides or other forms of environmental stress. Now there is abundant evidence that nematode

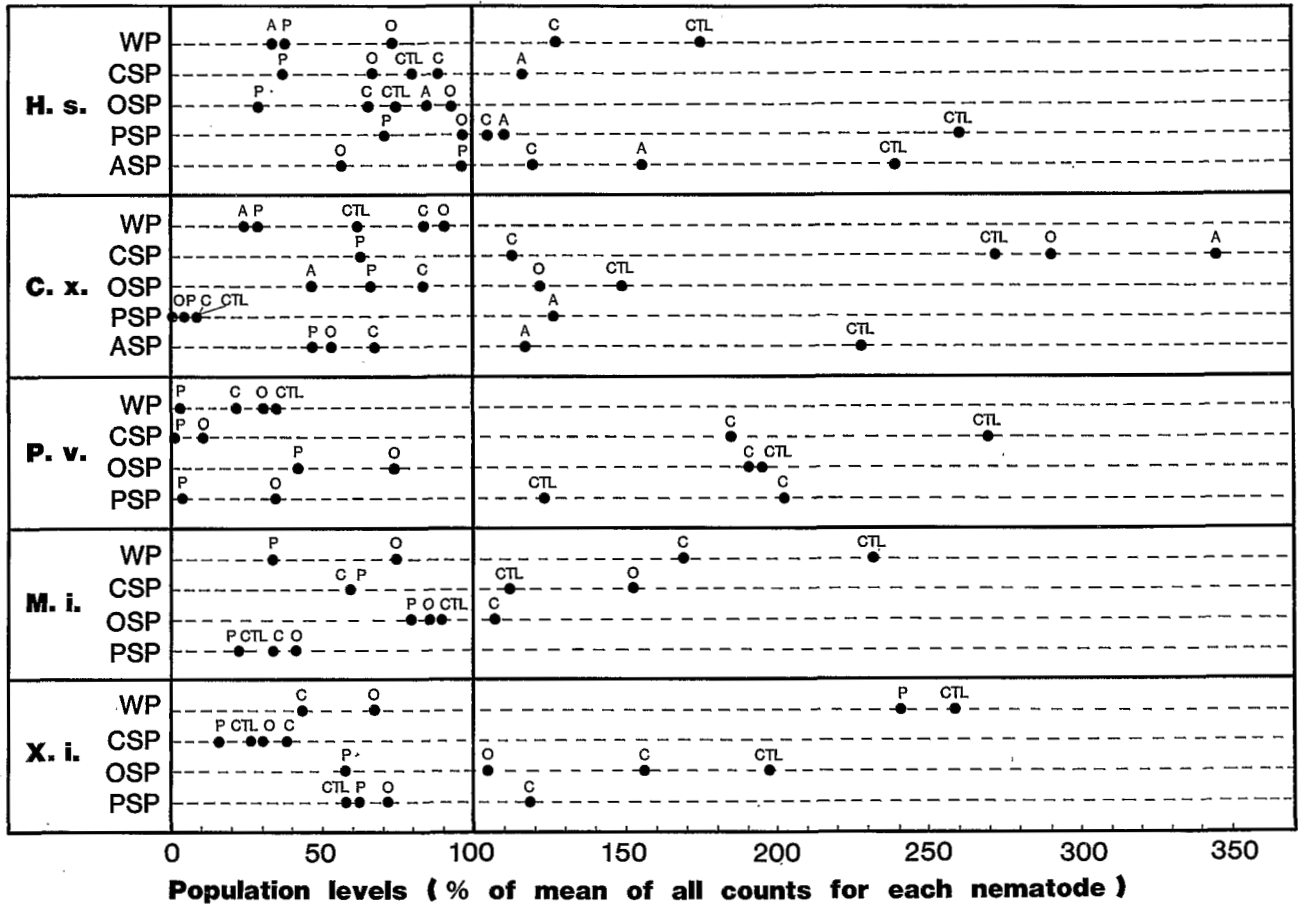


Fig. 1. Population levels as percent of overall mean for each nematode in treatments with different nematocides of nematode populations stressed with different nematocides at sublethal levels. A = Aldicarb, O = Oxamyl, C = Carbofuran, P = Fenamiphos, CTL = control = no treatment, WP = wild untreated population, CSP = carbofuran stressed population, OSP = Oxamyl stressed population, PSP = fenamiphos stressed population, and ASP = Aldicarb stressed population, H.s. = *Heterodera schachtii*, C.x. = *Criconebella xenoplax*, P.v. = *Pratylenchus vulnus*, M.i. = *Meloidogyne incognita*, X.i. = *Xiphinema index*.

Viglierchio & Schmitt, 1986; Yamashita, Viglierchio & Kuo, 1988b; Viglierchio, Brown & Kuo, 1989). Nematode species clearly respond differently to the same experimental protocol. While many stressed populations of different species removed from stress (CTL) explode to high population levels, an equal number remains below levels of other treatments. It is also evident that certain stressed populations develop higher population levels with certain nematocidal treatments than others.

Having accepted that nematodes adapt to prolonged pesticide stress, one may ask how long might this adaptation persist before reverting to the normal state with the stress pressures removed? The summary (Table 1) illustrates a trial conducted with *X. index* populations stressed five years and populations stressed three years, then unstressed, i.e., removed from stress for two years. It is clear with *X. index* that the adaptation effected by

pesticide stress persists in excess of two years. The most obvious manifestation in this case takes the form of enhanced reproductive capacity (Yamashita & Viglierchio, 1986b).

Moreover it can also be asked whether nematodes manifest intermediate or short-term responses to nematocides. One aspect of this question can be evaluated by immersing nematode populations of varied history in high concentrations (in the 0.5 mM range) of NFN, and assessing the response by changes in motility after 24 hours (Fig. 2). The responses of nematodes are widely varied depending not only on species, but also the preconditioning history of the population and the nematocide used for immersion (Yamashita & Viglierchio, 1986c, 1987a, 1988; Viglierchio & Brown, 1989). The results are in some cases similar to those seen in greenhouse trials, but in other cases not thereby indicating

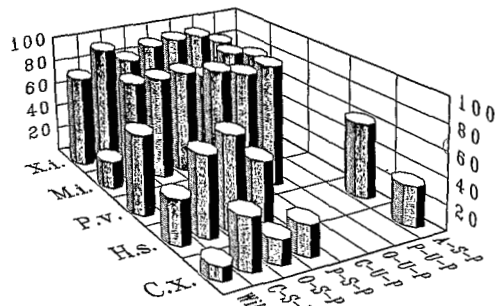
Table 1

Population levels of different *X. index* populations with different stressing histories, subjected to subnematicidal or no treatments, in terms of percent of populations increase of wild type.

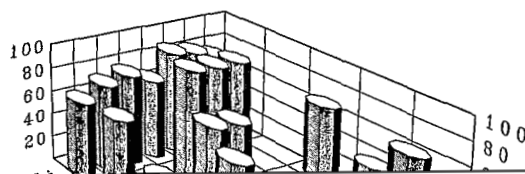
X. index Population	Control	Subnematicidal Treatment		
		C	O	P
C-S-P	11	11		
O-S-P	76		74	
P-S-P	23			52
C-U-P	67	78		
O-U-P	118		59	
P-U-P	266			135
Wild	100	69	92	97

C = Carbofuran, O = Oxamyl, P = Fenamiphos, C-S-P = C stressed population, O-S-P = O stressed population, P-S-P = P stressed population, C-U-P = C unstressed

CARBOFURAN



OXAMYL



followed by periodic assessments of motility by the *in vitro* method. The composite of such results (Fig. 3) whereby the responses of all induction treatments and *in vitro* immersions at the highest concentrations for all NFN are averaged, demonstrate for wild type *Pratylenchus vulnus* that the induction treatment provides for increased protection for 45 days. For wild type *X. index* protection increases for approximately two weeks, but decreases thereafter. Induction of stressed *X. index* populations provide slight if any protection whereas

Table 2

Effect of host on stressed and unstressed population structure of *Pratylenchus vulnus* as indicated by grape/bean ratios of different juveniles (J2, J3, J4) and adults (A).

Population	J2	J3	J4	A
CSP	2.80	1.90	.47	.32
CUP	1.10	3.10	.74	.24

nematodes, microorganisms, host plants. Therefore in pesticide treatments microorganisms would be subject to the same adaptive forces as nematodes. An early experiment (Yamashita, Viglierchio & Schmitt, 1986) using nematode free extracts of carbofuran and fenamiphos stock cultures of *X. index* confirmed the widely held belief that microorganisms could provide protection for the nematode population to subsequent nematicidal treatments. However, a later experiment targeting this phenomenon using nematicide-treated soils from *Heterodera schachtii* nematicide trials demonstrated no such activity, even in tests where the aerobic bacterial component was increased 3 000 fold over normal (Yamashita, Viglierchio & Kuo, 1988a). Field microbial degradation of nonfumigant nematicide was demonstrated by radio-carbon studies using treated soils from Costa Rican banana plantations (Anderson & Wybou, 1988). It is evident that soil microorganisms in banana plantations can degrade fenamifos after a lag period during which adaptation takes place (Fig. 4). Fenamifos degradation peaks directly after application. A related pesticide, Isophenphos, is degraded at a five-fold greater rate. The biomass degradative capacity in the absence of pesticide application in certain African fields, virtually disappears after seven months (Fig. 5). The facts suggest that soil microorganisms in general do not degrade soil applied nematicides; however, if those with potential degradative capacity occur, then prolonged pesticide stress encourages their adaptation as well as that of nematodes to provide additional protection to nematodes from nematicide application.

While the emphasis in studies of nematicide stress adaptation has involved plant-parasitic nematodes, the results are in agreement with those obtained with laboratory *in vitro* cultures of *Rhabditis oxyerca* reared on bacterial oatmeal cultures subjected to long-term exposures to Aldicarb and Oxamyl (Kampfe & Wischgoll, 1984). By gradually increasing the stressing concentrations, the nematodes after nine years could tolerate a 400-fold increase in Aldicarb concentration, and a 100-fold increase in Oxamyl. Aldicarb pretreatment increased tolerance to subsequent Oxamyl treatment while Oxamyl pretreated strains showed an increase in susceptibility to Aldicarb; moreover, there were signs of diminished activity in pretreated animals after transfer to nematicide-free media. Reproductive fitness was increased in stressed but not unstressed populations. The microflora of the culture appeared not to be altered by the nematicides. The adaptive changes reported with the bacterial feeding nematode are very similar to those reported for plant-parasitic nematodes.

Practical nematode control technology has fallen on hard times, with few effective and economical practices available. Most probably the late motivation for the types of research just described involves an improved understanding of behavioral relationships to fuel a generation of different and innovative tools to resolve

the problem. In this context they have been successful, for they do presage a hopeful future. The potential for the role of chemical agents for nematode control has never been greater, provided that primary attention is paid to the mode of action. For long-term effectiveness, each agent must have a characteristic mode of action, i.e., it must inhibit a different physiological system and yet meet environmental hazard constrictions including mammalian toxicity and pollution. Inasmuch as a primary premise for long-term sustainable nematode control strategy is dependent upon different modes of action, it is essential to secure an understanding of the fundamental target processes. Of the numerous options to gain this information two obvious ones include the determination of enzymic or protein changes, which reflect the mechanisms by which adaptation becomes expressed in nematode populations, and the testing for efficacy of a wide range of biochemical inhibitors evolved by colleagues in related disciplines of the biological sciences. Rudimentary steps have been taken in these directions, but they need to be extended much further (Veech, 1978; Glazer & Orion, 1985; Osman & Viglierchio, 1988; Viglierchio & Wu, 1989).

The potential for adaptability demonstrated to be inherent in pestiferous nematodes is not limited to chemical agents, but is a common integral element of natural adversarial relationships. Plant resistance has long been used as a component of pest management strategies. Experience has demonstrated that multiple gene based resistance is more stable while single gene based resistance whatever the mode of action, is rapidly thwarted by the adaptive processes, which also are often single gene based. To illustrate, the Mi gene, the essentially single gene resistance to major rootknot species, transferred to tomato from the wild type *Lycopersicon peruvianum* has been found to collapse under continued stress (Dalmasso, pers. comm., 1988). Although aggressive field populations have been found occurring naturally in California, Mexico, Africa, and elsewhere, it has been shown that a non-aggressive population inoculated to Mi gene based resistant tomato develops an aggressiveness in three generations that is rapidly lost upon return to normal tomato, however, after some 30 generations on the resistant tomato, the aggressiveness is lost very slowly, if at all.

Biological control methods which are currently receiving appreciable emphasis are also subject to the vagary of adaptive forces. Although adaptability in this area has not been demonstrated as yet with nematodes, entomologists have indicated that lepidopterous larval stages subjected to control measures using *Bacillus thuringiensis* are developing resistance.

In conclusion, the available evidence for nematode control by means of chemical or biological agents and single gene based plant resistance is consistent with the entomologically based empirical five year rule viz., any management tactic under single gene control and used

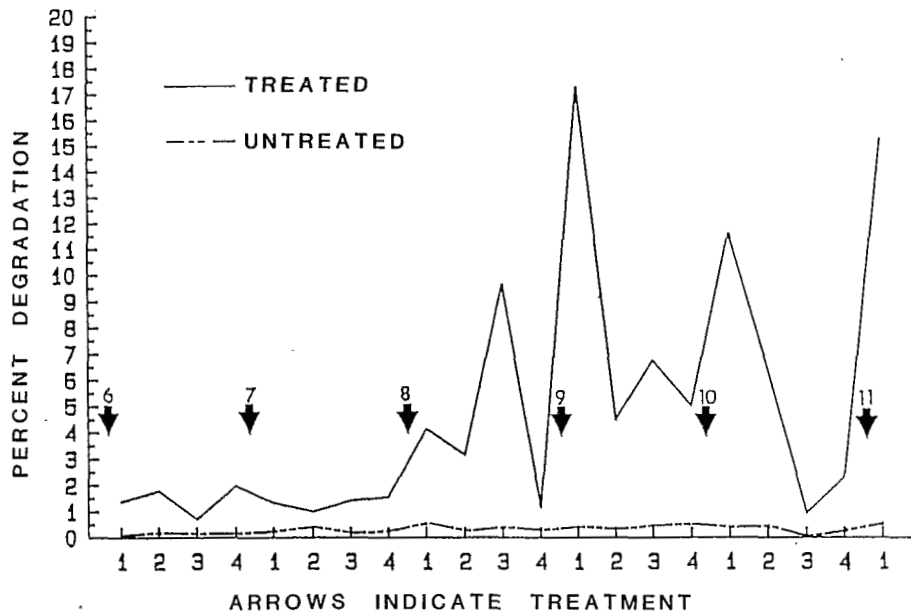


Fig. 4. Degradation of fenamifos in fenamifos treated soils from Indiana Tres, Costa Rica. Treatments applied at four month intervals, sampling for degradation analysis done monthly (After Anderson & Wybou, 1988).

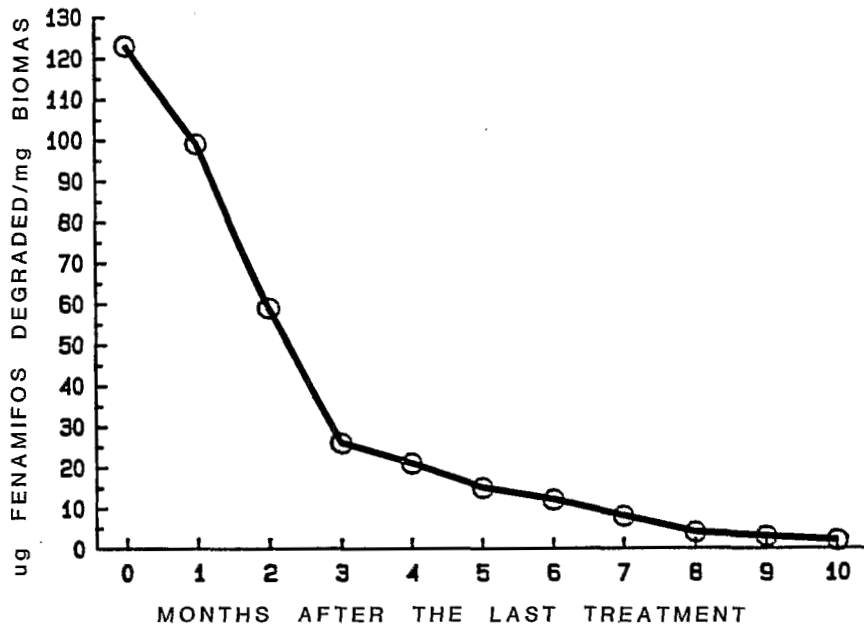


Fig. 5. The recovery time to normalcy after treatment termination of a banana fenamifos problem soil from the Ivory Coast. Treatment = 40 kg a.i./Ha/yr (After Anderson & Wybou, 1988).

continually is subject to failure within five to fifteen generations of the pest, or usually about five years. Unless the philosophy and the strategy of management or control changes to conform to and work in concert with nature's forces, past mistakes and failures will continue to be repeated.

The expectation that any single agent will be effective in controlling all nematodes is largely fantasy. A revised view requires that different agents, having different

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