The behavior of nonfumigant nematicide-stressed, unstressed and wild populations of *Pratylenchus vulnus* cultured on grapevines and bean plants

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SUMMARY

Several stock cultures of *Pratylenchus vulnus* were kept on Thompson Seedless grapevines. These stock cultures were separated into groups and each group was stressed for five years with subnematicidal doses of the nonfumigant nematicides carbofuran, oxamyl and phenamiphos. One half of each population group was then released from stress for one year (unstressed). Nematodes from each of the stressed and unstressed populations were cultured on bean plants. All the stressed and unstressed nematodes developed lower population levels than did the wild population. However, the percentage of each nematode population found in the root tissue (as opposed to soil) was lowest in the wild population. The initial population structures of various nematodes stages was used as a character. Based on this character, each of the various populations displayed distinct differences when cultured on grapevines. These differences tended to be masked when the various populations were cultured on bean plants. Unstressing appeared to alter population levels and population structures. However, this varied with the specific nematode population and specific host. The characteristics of population levels, percent adults found in root tissue and percent of the total population found in root tissue were closely correlated (r = 0.992).

RÉSUMÉ

Le comportement de populations de Pratylenchus vulnus *sensibilisées
à un nématicide non fumigant, désensibilisées, et sauvages, élevées sur vigne et sur haricot*

Plusieurs élevages de masse de *Pratylenchus vulnus* ont été maintenus sur vigne « Thompson seedless ». Ces élevages ont été divisés en groupes dont chacun a été sensibilisé pendant cinq années à des doses sublétales de produits nématicides non fumigants : carbofuran, oxamyl et phenamiphos. La moitié de chacune de ces populations a été ensuite retirée de l'action de sensibilisation (population désensibilisées). Les nématodes provenant de chacune des populations sensibilisées et désensibilisées ont été élevés sur haricot; les nématodes provenant de ces deux types de population atteignent des niveaux de population inférieurs à ceux de la population sauvage. La structure de la population, quant aux différents stades des nématodes, a été utilisée comme caractère différentiel; en se fondant sur celui-ci, chacune des populations montre des différences distinctes lorsqu'elles sont élevées sur vigne; par contre ces différences tendent à s'estomper dans le cas d'élevage sur haricot. La désensibilisation paraît modifier les niveaux et structures des populations; cependant ce phénomène varie pour une population et un hôte donnés. Les caractéristiques liées aux niveaux des populations, au pourcentage d'adultes observés dans les racines et au pourcentage de la population totale présent dans les racines sont très étroitement corrélées (r = 0,992).

In an earlier study stock cultures of *Xiphinema index*, *Meloidogyne incognita* and *Pratylenchus vulnus* were stressed monthly with subnematicidal levels of carbofuran, oxamyl and phenamiphos (Yamashita, Viglierchio & Schmitt, 1985). After more than three years of stressing, the populations were tested for any possible changes in their responses to nematicidal-level treatments. Alterations in population behaviors which surfaced included characters such as resistance, increased susceptibility, changes in reproductive potential and habituation. Subsequently, stressed population cultures of *X. index* were released from stress for one year and

tested in the same manner for the stability of these altered behaviors (Yamashita & Viglierchio, 1985). Depending upon both the specific unstressed population and the specific nematicides used for testing, various results were observed. These results included such characteristics as the retention of altered behaviors, a reversion to wild type, extreme reversals in behavior and signs of increased reproductive potential.

The last ten years has witnessed a dramatic shift from the use of fumigants to that of nonfumigant nematicides. Along with this change has come the rising costs in agriculture. Farmers today are turning to professional

advisors. Their dealings with plant-parasitic nematode problems places much emphasis on the " economic threshold " level. Resulting control programs are frequently staggered. This may result in a field being treated for a couple of years, followed by a lag period and then treated some years later.

The economic importance of the plant-parasitic nematodes *M. incognita* and *P. vulnus* is well recognized. As mentioned earlier, when stressed with nonfumigant nematicides for over three years, these species displayed a number of behavioral changes. However, a realistic approach to characterizing the responses demands the practical considerations of behavioral change persistence. This study was conducted to test the stability of some behavioral changes by comparing stressed, unstressed and wild populations. It was also designed to characterize the complex nature of nematode-host-nematicide interactions.

Materials and methods

Meloidogyne incognita : Unstressed population stock cultures were started in the same way as for *X. index* (Yamashita & Viglierchio, 1985). Unstressed stock pots were further expanded by inoculating two month old French Colombard grapevines with J 2 larvae. After two years, without subnematicidal stressing, the stock cultures were extracted for J 2 larvae. However, the number of J 2 larvae were found to be very low and infected with an organism resembling *Pasteuria penetrans*. The cultures were salvaged by sterilizing egg masses and inoculating emerged J 2 larvae onto Murietta tomato plants. These were left to rebuild for later testing.

Pratylenchus vulnus : Unstressed populations were started and later expanded into a total of four stock pots per population. The method was the same as for *M. incognita*. After the first two years of stressing, the cultures were repotted onto young Thompson Seedless grapevines. This was done with an inoculum of about 1,000 mixed-stage nematodes. Sterile autoclaved soil and pots were used in all cases. After the fourth year of stressing, one half of the stock cultures were removed from monthly subnematicidal stressing. Two stock culture pots from each stressed population were removed from monthly treatment. These were expanded to four pots per population by inoculating two month old Thompson Seedless grapevines with an aliquant of 500 mixed-stage nematodes (extracted from soil and root plugs from the original stock culture pots). The following concentrations of nonfumigant nematicides were being used before being released from monthly subnematicidal stressing : Carbofuran at 0.002 mM; Oxamyl at 0.005 mM; Phenamiphos at 0.0016 mM.

After one year, the unstressed populations were inspected for nematode numbers and found to be too low for conducting a full-scale greenhouse test (as was done

for *X. index*). As a result, all stressed and unstressed stock cultures of *P. vulnus* were extracted for population level inspections. Because of the low nematode numbers found, a test was designed to compare population level and structural changes. The phenamiphos-stressed population levels were found to be extremely low and this population was omitted from the tests. Nematodes from stressed and unstressed cultures were first evaluated for population structure. That is, the percent contribution from each nematode stage was recorded. Criteria used to distinguish J 2, J 3, J 4 and adult stages were outlined by Chitambar (1983). Adults were easily distinguished. Larval stages were separated mostly by size comparisons and when necessary supplemented with observations on the development of the genital primordia.

Two week old Kentucky Wonder bean plants (in 500 cm³ styrofoam cups), were inoculated with an aliquant of 340 mixed-stage nematodes from each stock population. Being a more suitable host than grapevines, the beans were selected here to accelerate population increases. Five cups were inoculated for each stressed and unstressed population. Another five cups were inoculated with nematodes taken from a wild population culture. The inoculated beans were maintained in a greenhouse and watered twice daily with half strength Hoagland's solution. This test did not involve the application of nonfumigant nematicides. Rather, the various populations were allowed to develop on the beans in the absence of any chemical stressing. The greenhouse temperature was maintained at about 25° throughout the test. A randomized complete block design was utilized.

Following 40 days of growth, the bean plants were harvested. Nematodes in soil were extracted using 246 µm and 38 µm sieves. Roots from each plant were cut into 1 cm pieces and misted for five days. The suspension from the soil and roots were evaluated separately. Each nematode suspension was brought up to 50 mls and three 2 ml aliquants were evaluated for J 2, J 3, J 4 and adult population numbers. The total population numbers, their structure and percent distribution in the soil *vs.* roots were recorded for analyses. Population number differences between various stock cultures were evaluated following a Log_{10} (X + 1) transformation. Analysis of the population structure and percent nematodes in roots was conducted following an arcsine transformation. Mean comparisons were conducted using Duncan's Multiple Range test. An upper level of significance of 5 % was used in these analyses. Relationships between stock populations, total populations and percent distribution in the roots were evaluated using correlation and regression for three variables.

Results

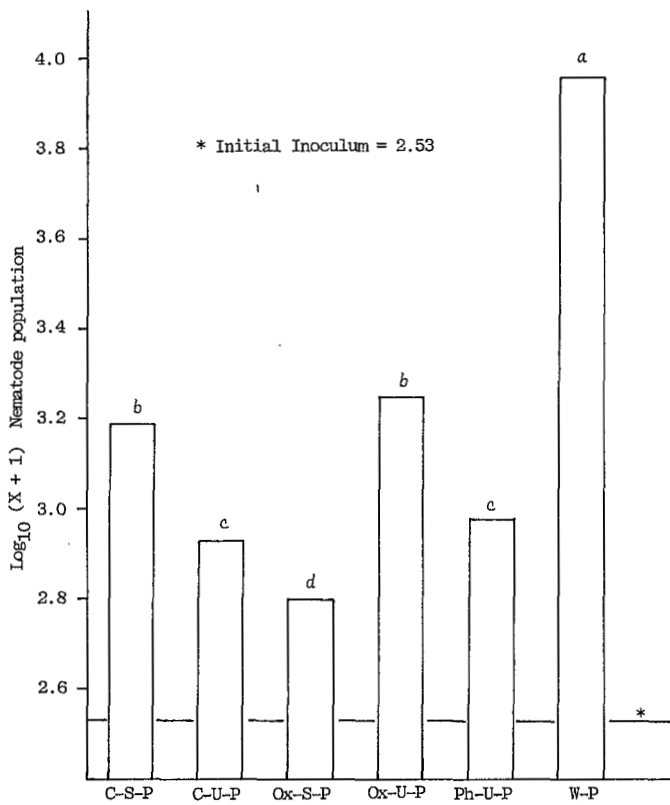The low stock culture population levels made it necessary to conduct tests with *P. vulnus* differently

Fig. 1. Mean nematode numbers from various populations of *Pratylenchus vulnus* cultured on bean plants for 40 days at 25°. Means not followed by a common letter are significantly different at an α level of 5 % or less.
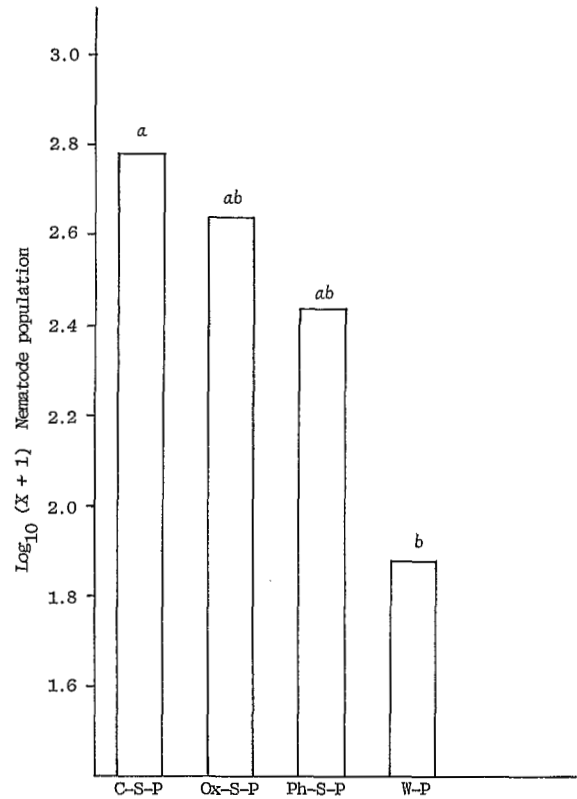

Fig. 2. Mean nematode numbers from stressed and wild populations of *Pratylenchus vulnus* cultured on Thompson Seedless grapevines for 60 days at 25°. Means not followed by a common letter are significantly different at an α level of 5 % or less.
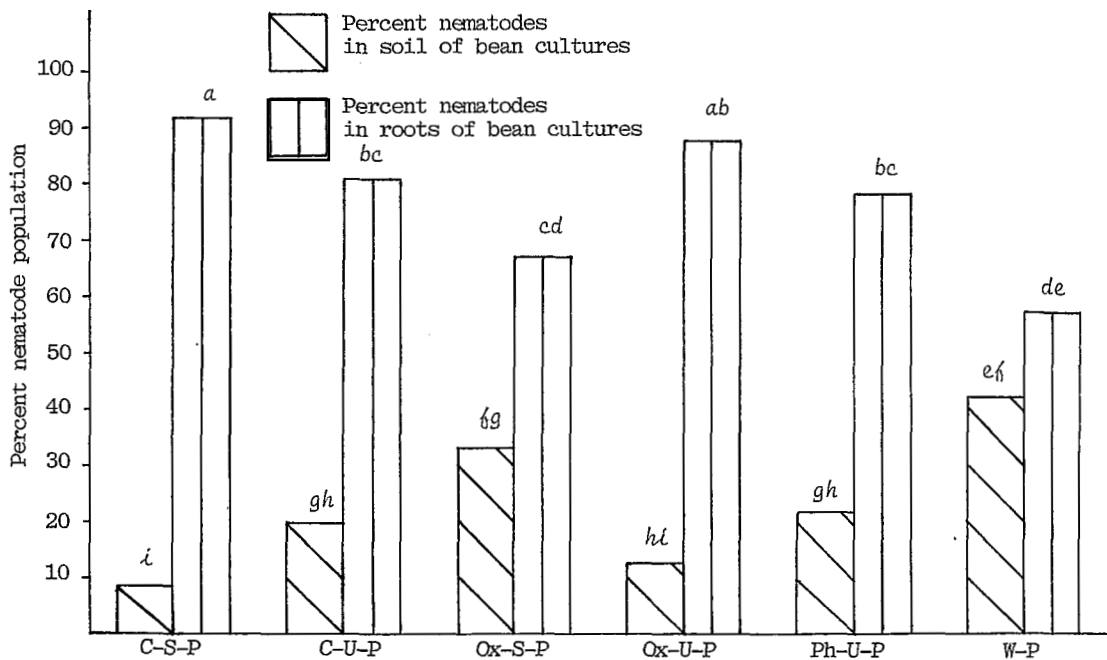

Fig. 3. The percentage of each *Pratylenchus vulnus* population found in the soil and roots of bean cultures. Means not followed by a common letter are significantly different at an α level of 5 % or less.

Table 1

Population levels from stressed and unstressed stock cultures
of *Pratylenchus vulnus* reared on grapevines

P. vulnus population	Mean population levels per culture pot	Duncan's MRT
Stressed population :		
C-S-P	7 050	A
Ox-S-P	2 667	B
Ph-S-P	45	D
Wild	520	C
Unstressed population :		
C-U-P	3 425	a
Ox-U-P	1 108	b
Ph-U-P	340	c
Wild	520	c

Numbers represent the mean nematode levels from four stock culture pots. At the time of population level inspections the stressed populations had received monthly subnematicidal stressing for 60 months. The unstressed populations has been released from stress for 12 months. Means not followed by a common letter are significantly different at an α level of 5 % or less.

Table 2

Comparisons between stages of *Pratylenchus vulnus* from parent stock populations cultured on grapevines

P. vulnus population	Nematode Stages			
	J2	J3	J4	A
C-S-P	31 de	41 c	19 hi	9 j
C-U-P	10 j	55 b	26 efg	9 j
Ox-S-P	23 fgh	34 d	28 ef	15 ij
Ox-U-P	21 gh	61 a	14 ij	4 k
Ph-U-P	14 ij	50 b	23 fgh	12 ij
W-P	8 jk	43 c	41 c	8 jk

Means represent the percent representation of each nematode stage within each population cultured on grapevines. Means not followed by a common letter are significantly different at an α level of 51 % or less.

from those conducted with *X. index* (Yamashita & Viglierchio, 1985). The immediate tests with *P. vulnus* did not involve treatment with nematicides. As a result, detection of differences between stressed, unstressed and wild populations relied upon the following observations :

Differences in population levels of nematodes.

Comparisons between nematodes stages from parent

stock populations cultured on grapevines and bean plants.

Comparisons between populations : total percentage of nematodes extracted from bean roots and soil.

Comparisons between the percentages of each nematode stage extracted from bean roots.

Interrelationships between total population levels, percent adults in the roots and the total percent of nematodes found in the roots.

The following abbreviations will be used throughout the paper :

C-S-P	=	Carbofuran-Stressed Populations
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

DIFFERENCES IN POPULATION LEVELS OF NEMATODES

Population levels of each stock culture population are summarized in Table 1. Each value represents the mean population level of four stock culture pots. The initial inoculum used to start the stressed populations was different from that used to start unstressed populations. As a result, the means of the stressed and unstressed populations were analyzed separately. At the time this population inspection was conducted, the stressed populations had been maintained for five years. The unstressed populations were exactly one year old.

As can be seen from Table 1, the consistent order from highest to lowest population levels is : stressed population : 1 : C-S-P; 2 : Ox-S-P; 3 : W-P and 4 : Ph-S-P and W-P; unstressed populations : 1 : C-U-P; 2 : Ox-U-P; 3 : Ph-U-P and W-P. These results appear to coincide closely with the trends observed in Figure 2 (1 : C-S-P; 2 : Ox-S-P; 3 : Ph-S-P; 4 : W-P), which were recorded with four year old stressed populations. In most instances the stressed and unstressed population levels exceeded those of the W-P.

The population levels from six *P. vulnus* populations are summarized in Figure 1. On bean plants the W-P (9,120) reached the highest numbers. This was significantly larger than all other populations tested. However, in an earlier study on stressed populations cultured on Thompson Seedless grapvines (Yamashita, Viglierchio & Schmitt, 1985), the reverse effect was observed (Fig. 2). It appears that the behavior of specific populations of *P. vulnus* is largely influenced by the specific host. On grapevines the W-P level (76) was lowest and significantly below the C-S-P control levels (605).

As mentioned in the material and methods section, the Ph-S-P cultures were found to be extremely low. They were found to be contaminated with root-knot

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Table 3

Comparisons between stages of *Pratylenchus vulnus*
from populations cultured on bean plants

P. vulnus population	Nematode Stages			
	J2	*J3*	*J4*	*A*
C-S-P	11 *fg*	22 *d*	39 *b*	28 *c*
C-U-P	9 *g*	18 *e*	35 *b*	38 *b*
Ox-S-P	9 *g*	16 *ef*	39 *b*	36 *b*
Ox-U-P	3 *h*	25 *ed*	45 *a*	27 *cd*
Ph-U-P	7 *gh*	16 *ef*	40 *ab*	37 *b*
W-P	15 *ef*	18 *e*	38 *b*	29 *c*

Means represent the percent representation of each
nematode stage within each population cultured on bean
plants. Means not followed by a common letter are
significantly different at an α level of 5 % or less.

Table 4

Comparisons between the change in *Pratylenchus vulnus*
juvenile and adult stages as the host is changed
from grapevines to bean plants

P. vulnus population	Δ In nematode Stages : Growth on Grapevines-Beans			
	Δ J2	*Δ J3*	*Δ J4*	*Δ A*
C-S-P	20 *bc*	19 *c*	— 20 *ij*	— 19 *ij*
C-U-P	1 *f*	37 *a*	— 9 *gh*	— 29 *l*
Ox-S-P	14 *d*	18 *cd*	— 11 *h*	— 21 *ijk*
Ox-U-P	18 *cd*	36 *a*	— 31 *l*	— 23 *jk*
Ph-U-P	7 *e*	34 *a*	— 17 *l*	— 24 *k*
W-P	— 7 *g*	25 *b*	3 *f*	— 21 *ijk*

Numbers represent the difference between mean
percentages (% contribution from nematode stages grown on
grapevines minus % contribution from nematode stages grown
on bean plants). Numbers not followed by a common letter are
significantly different at an α level of 5 % or less.

nematodes and the exact cause of the low populations
cannot be evaluated at this time. However, it is possible
to compare the effects of unstressing with the C-S-P *vs.*
C-U-P and Ox-S-P *vs.* Ox-U-P comparisons (Fig. 1).
Removing the C-S-P (1,445) from stress for one year
appears to affect population levels, as the C-U-P (797)
is significantly lowered. The opposite effect is seen with
the Ox-S-P. Removing the Ox-S-P from stress appears
to improve population build-up (Ox-S-P = 603 *vs.*
Ox-U-P = 1,738). While the Ph-U-P cannot be com-
pared to its respective stressed population, the levels
(933) were found to be significantly larger than the
Ox-S-P (603; Fig. 1). On bean plants the decreasing

order of population levels were found to be : 1 : W-P;
2 : C-S-P and Ox-U-P; 3 : C-U-P and Ph-U-P; 4 :
Ox-S-P. However, as mentioned earlier, it is important
to consider the host in these evaluations. In an earlier
study, using Thompson Seedless grapevines, the W-P
levels reached the lowest numbers (Fig. 2).

COMPARISONS BETWEEN NEMATODE STAGES FROM PAR-
ENT STOCK POPULATIONS CULTURED ON GRAPEVINES
AND BEANS

In each stock population cultured on grapevines, the
largest proportion of nematodes appears to be represen-
ted by J 3 larvae (Tab. 2). This is followed by either the
J 4 or J 2 larvae, with adults forming the smallest seg-
ment of the population. When cultured on beans for 40
days, however, the general structure is seen to change
(Tab. 3). The J 4 larvae now form the largest segment
of the populations, followed by the adults and J 3 larvae,
with the J 2 larvae representing the smallest portion of
each population. The larger increase in the proportion
of adults is evident in the bean cultures. They form a
distinctly larger segment of each bean cultured popula-
tion than is represented in the grapvine cultured popula-
tions. Another effect, which is quite consistent, involves
comparisons between the stressed and unstressed popu-
lations. When grown on grapevines, there appears to be
significant differences in the population structures
between C-S-P *vs.* C-U-P and the Ox-S-P *vs.* Ox-U-P
(Tab. 2). In addition all stressed and unstressed popu-
lations appear to have differences in population struc-
ture from the W-P (Tab. 2). There is a slight tendency
for differences between stressed and unstressed popu-
lations cultured on bean plants, as well (Tab. 3).
However, these population structure differences are
both of lower frequency and magnitude. In earlier
studies grapevines were observed to be a less suitable
host than bean plant for *P. vulnus* population build-up.
These differences might otherwise have been masked
when cultured on the more suitable bean host. The
populations cultured on grapevines show distinct signs
of structural differences. These differences indicate
unique characteristic of each population. However,
when the same populations are cultured on bean plants,
their population structures appear to be more uniform
(Tab. 3).

The percent representation of each nematode stage
for each population is presented in Tables 2 and 3. The
mean differences between the values from grapevine
cultures minus the values from bean cultures is pre-
sented in Table 4. When populations are extracted from
grapevines and cultured on bean plants, the general
trend is a distinct increase in J 4 and adult stages (Tab.
4). This is indicated by the many negative values in these
columns. The reverse effect occurs with the J 2 and J 3
stages. Their positive values indicate decreases in these
stages when cultured on bean plants. An exception to

Table 5

Percentage of each stage of *Pratylenchus vulnus* extracted from roots of bean plants

4.3,4.6,3.6,3.6,3.6 P. vulnus population	Nematode Stages			
	J2	*J3*	*J4*	*A*
C-S-P	99 *a*	94 *abc*	95 *ab*	90 *abcde*
C-U-P	98 *a*	96 *a*	74 *efgh*	78 *bcdefg*
Ox-S-P	56 *ij*	59 *hij*	79 *bcdefg*	65 *fghij*
Ox-U-P	77 *cdefg*	92 *abcd*	88 *abcde*	87 *abcde*
Ph-U-P	99 *a*	82 *abcdef*	75 *defgh*	75 *defgh*
W-P	48 *j*	68 *fghi*	58 *hij*	61 *ghij*

Means represent the percentage of each nematode stage extracted from bean roots (the balance being extracted from the soil). Numbers not followed by a common letter are significantly different at an α level of 5 % or less.

these general trends is found with the W-P. While other populations decreased in the percent of J 2 larvae, the W-P displayed a significant increase (7).

Within each population the changes that occur in each stage appears to be significant for almost all populations. The only two exceptions are the low degree of change observed with the J 2 larvae of the C-U-P (1) and the J 4 larvae of the W-P (3).

COMPARISONS BETWEEN POPULATIONS: THE TOTAL PERCENT OF NEMATODES EXTRACTED FROM BEAN ROOTS AND SOIL

With all *P. vulnus* populations, the great majority of nematodes are found in the roots (Fig. 3). Highest values are found in the C-S-P (92 % from roots) and the lowest values are found in the W-P (57 % from roots). Except for the Ox-S-P (67 % from the roots), all other populations show significantly higher percentages of nematodes found in the roots than the W-P.

In addition, unstressing appears to have affected these values. Percentages of nematodes from roots in the C-S-P are significantly larger than from the C-U-P (92 % vs. 81 %). The effects of unstressing are reversed with the Ox-S-P. Here, the percentage of nematodes found in the roots of the Ox-S-P are significantly lower than found in the Ox-U-P (67 % vs. 87 %).

COMPARISONS BETWEEN THE PERCENTAGES OF EACH NEMATODE STAGE EXTRACTED FROM THE ROOTS

Fairly uniform percentages of the C-S-P nematode stages were extracted from bean roots (Tab. 5). However, other populations did show some signs of

variations. Although there are exceptions, the main differences between stages appears to occur with J 2 and J 3 larvae *vs.* J 4 and adults. All values from the W-P appear to be lower than most percentages from other populations. This is reflective of the low total percentage of W-P nematodes found in roots (Fig. 3). Except for the low percentage (48 %) of J 2 larvae found in roots, all other stages of the W-P appear quite uniform.

Unstressing appears to affect these values in the C-U-P and Ox-U-P quite differently. With the C-U-P unstressing significantly reduces the percentage of J 4 larvae found in bean roots (95 % vs. 74 %). However, unstressing appears to increase the percent of J 2, J 3 and adults in the Ox-U-P (J 2 - 56 % vs. 77 %; J 3 - 59 % vs. 92 %; A - 65 % vs. 87 %). These effects of unstressing on changes in percentage of nematode stages found in roots (Tab. 5) were believed to be correlated to the original proportions of each stage (Tab. 2, Tab. 3). However, no significant correlations were detected. Thus, the reduction or increases in the percent of nematode stages found in bean roots (C-U-P and Ox-U-P) are believed to be a result of unstressing effects.

INTERRELATIONSHIPS BETWEEN TOTAL POPULATION LEVELS, PERCENT ADULTS IN THE ROOTS AND THE TOTAL PERCENT OF NEMATODES FOUND IN THE ROOTS

When observing the population data (Fig. 1) and the total percent of nematodes in bean roots (Fig. 3), certain correlations were apparent. The most striking of these was the observation that the highest and lowest population levels (W-P and Ox-S-P; Fig. 1) both had the lowest percent of nematodes in bean roots (W-P = 57 %, Ox-S-P = 67 %; Fig. 3). Populations with intermediate levels of nematodes (Fig. 1) appeared to have intermediate percentages of nematodes found in bean roots (Fig. 3).

Several correlation and regression analysis studies of these observations proved to be incomplete. However, use of a third character (the percent adults in bean roots) provided for a highly significant multiple correlation coefficient ($r_{yx1.x2}$ = 0.992). The Log_{10} of the total population level (x_1) and the arcsine transformed percent adults found in roots (x_2) were used as characters of each population. These two characters were found to account for more than 98 % of the variability in the total percent of nematodes found in bean roots (y). The regression equation proved to be a near perfect fit (y = 30.77 − 6.844 x_1 + 0.892 x_2).

Discussion

DIFFERENCES IN POPULATION LEVELS OF NEMATODES

The general pattern of population levels seen in stock cultures (Tab. 1) and from control pots of an earlier test

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(Fig. 2) appear to be manifestations of true population character differences. There are other possible explanations but these do not coincide with past and immediate test results. For example, population levels of a related species, *Pratylenchus penetrans*, were increased in the presence of certain species of fungi (Edmunds & Mai, 1966; Mountain & McKeen, 1962). Secondly, in certain instances, the fungal and general microbial population levels were shown to be increased following applications of carbofuran, oxamyl and/or phenamiphos (Mathur, Hamilton & Vrain, 1980). Furthermore, it appears that fungi are capable of readily metabolizing nonfumigant nematicides (Jones, 1976), and the role of microbes in pesticide degradations has been well documented (Kaufman & Edwards, 1982). In an earlier study addition of stock culture leachings to test pots were shown to either enhance population decreases or provide protection from nematicidal-level treatments (Yamashita, Viglierchio & Schmidtt, 1985). There is a tendency, then, to attribute population level differences to microbial-related factors. The major discrepencies in this explanation lies in two major observations : i) While stock population levels (Tab. 1) may be subject to microbe-related factors, the coinciding population levels of control grapevine test pots (Fig. 2) are not. The test pots in this latter case did not receive additions of leachings or nematicides. ii) The W-P levels, which were never treated with nematicides, are consistently low.

As another example, the concept and role of " suitable " and " unsuitable " hosts in differential population levels is well understood. The various biochemical mechanisms of this plant incompatibility factor has been reviewed (Giebel, 1979; Kaplan & Keen, 1980). Also, in certain instances, a moderately suitable host can be made highly suitable, with increased nematode numbers. Practices that reduce plant dry weight, such as suboptimal lighting, temperature, nutrients and the pruning of plants parts have been shown to contribute to nematode population build-ups (Dolliver, 1961). This coincides with studies which show that an optimal plant nutritional status can increase resistance to nematode parasitization (Zinov'eva *et al.,* 1978). Since applications of some nonfumigant nematicides have been shown to alter normal plant physiological processes (Franco & Duran, 1981; Milne, Van Lelyveld & Villiers, 1977; Sarah, 1981; Steifert & Davidek, 1978), then, there may be a tendency to attribute the different population levels (Tab. 1; Fig. 2) to indirect host effects. However, there are two general discrepancies in this explanation : i) Population levels recorded from the grapevine test posts (Fig. 2) and from the unstressed stock cultures (Tab. 1) were free of nematicide treatments; ii) Other differences between populations, such as population structure (Tab. 2; Tab. 3); population structural changes (Tab. 4) and the percent of nematodes found in roots (Fig. 3; Tab. 5) give further indications that the various populations are

different.

It is common knowledge that certain hosts are better suited for some plant-parasitic nematodes. A host range study for *P. vulnus* gave indications that this species did not behave differently (Jensen, 1953). When cultured on grapevines, the W-P levels reach a low 76 nematodes per culture pot (Fig. 2). With a smaller initial inoculum on bean plants (500 on grapevines *vs.* 340 on bean plants), however, the W-P reaches the highest population levels (9,120; Fig. 1). The highest levels reached on the grapevines (C-S-P at 603 nematodes per pot; Fig. 2) are comptable to the lowest population levels reached on bean plants (Ox-S-P at 631 nematodes per pot; Fig. 1). The concept of a more " suitable " host may explain the sudden increase of the W-P on bean plants. It cannot, however, totally explain why the stressed and unstressed populations did not comparably increase in their numbers. If results of the growth of the Ph-S-P on beans were obtainable, perhaps, it might coincide with population level trends seen on grapevines (from highest to lowest — C-S-P, Ox-S-P, Ph-S-P). This consistency in the trend of population level behavior (of the stressed populations) would then lend greater support to population characterization. However, the order of population levels in unstressed populations on grapevines (C-U-P, Ox-U-P, Ph-U-P; Tab. 1) does not coincide with the population level order from bean plants (Ox-U-P, Ph-U-P & C-U-P; Fig. 1). Apparently, there are unique interactions between a specific host and a specific population of nematodes. Without further research on these associations it would be difficult to characterize these populations outside of general observed trends.

A factor which may prove important in these evaluations is the concept of nematode races. This implies high levels of specificity in nematode-host interactions. The authors believe that long-term subnematicidal stressing may have selected for highly specific races of *P. vulnus.* The selective pressures were governed by the specific nematode-host-nematicide interactions. Insect-insecticide interactions, alone, are known to be of a dynamic and multidimensional complexity (Welling, 1977). Between various nematode races alone, there may possibly be differences in enzymes used in feeding and digestion, nerve transmission enzymes, surface lectins and fecundity, to name a few. A specific race, which does well on one host treated with one particular nematicide, may not behave the same when the host and/or the nematicide is changed. This can be seen with the C-S-P and C-U-P (Fig. 1). Nematodes taken from C-S-P cultures, continually stressed with carbofuran, develop significantly larger population levels on bean plants than the C-U-P. Release from carbofuran stressing for one year appears to alter the fitness of the C-U-P when placed on beans. The unique nature of this shift can be appreciated when noticing that an opposite effect occurs

with the Ox-S-P and Ox-U-P (Fig. 1). Here, releasing the nematodes from oxamyl stress appears to contribute towards a slight reversion to wild-type (Ox-S-P at 631 *vs.* Ox-U-P at 1,778), although the fitness of the Ox-U-P on bean plants cannot match the fitness of the W-P (Ox-U-P at 1,778 *vs.* W-P at 9,120). Since *P. vulnus* is known to reproduce by amphimixis (Roman & Triantaphyllou, 1969), opportunity for the evolution of highly specific races would seem possible.

COMPARISONS BETWEEN NEMATODE STAGES FROM PARENT STOCK POPULATIONS CULTURED ON GRAPEVINES AND BEANS

When carrot callous tissue cultures are inoculated with mature females and males of *P. vulnus*, the various stages appear as follows; J 2 at nine days from inoculation; J 3 at eleven days from inoculation; J 4 at seventeen days from inoculation; adults at eighteen days from inoculation (Chitambar, 1983). In spite of small time requirement differences for each stage development, the structure at equilibrium should be relatively balanced with higher representations from J 2 and adults. This is so, because : *i)* Adults have a longer life span than all other stages, *ii)* A certain percent of J 2 larvae will be found accumulating in the soil and without invading the roots may remain in a J 2 state. This structure trend was observed with *P. vulnus* cultured on carrots for 90 days (Marban-Mendoza & Viglierchio, 1980).

All stock populations of *P. vulnus* (stressed, unstressed and wild) were cultured on Thompson Seedless grapevines under similar conditions for more than one year (stressed for five years; unstressed for one year; wild for five + years). This should have allowed existing populations to reach an equilibrium in their structure. The consistently large J 3 representation of all grapevine cultures indicates that the J 3 to J 4 transition may be slightly affected on this host (Tab. 2). The disruption of this transition seems to be overcome when the populations are cultured on bean plants. A differential effect of the host on specific stage development may in part indicate the unique physiology of each stage. The greater degree of differences seen both within and between grapevine cultures (as opposed to bean plant cultures) is indicative of the specific interactions of each population and each stage with that particular host. The monthly subnematicidal treatments in stressed cultures adds to the complexity and specificity of these interactions during the natural selection process. Being a less suitable host than bean plants, the grapevines contribute to the expression of existing differences between populations and even between stages within a population.

COMPARISONS BETWEEN PERCENTAGES OF NEMATODES EXTRACTED FROM ROOTS

The ability for a *P. vulnus* population to parasitize the root system can be inferred from evaluating the total percentage of nematodes extracted from the roots. Studies conducted with a related species, *Pratylenchus penetrans*, have correlated suboptimal conditions of both the host and nematode with the migration out of the roots to soil (Patterson & Bergeson, 1967). With corn, for example, the number of *P. penetrans* adults extracted from the soil was inversely corelated to the population extracted from the roots (Miller, Boothroyd & Mai, 1963). Under the conditions of this experiment, the total percent of nematodes extracted from roots was found to be correlated to both the population levels and the percent adults extracted from the roots. The correlation and regression in three variables and the regression equation were used mainly to help characterize the different populations. The subcharacter of percent adults extracted from roots was used to help facilitate this characterization. The correlation and regression studies do not in themselves propose cause and effect relationships.

Unstressing appears to decrease the percent of J 4 larvae in the C-U-P (Tab. 5; J 4 — 95 % to 74 %) while increasing the J_2, J_3 and adult stages in the Ox-U-P (Tab. 5; J 2 — 56 % to 77 %; J 3 — 59 % to 92 %; A — 65 % to 87 %). These changes are related to the effects of unstressing in the reductions of the C-U-P (Fig. 1; C-S-P at 1,549 *vs.* C-U-P at 851) and the increases in the Ox-U-P (Fig. 1; Ox-S-P at 631 *vs.* Ox-U-P at 1,778). The effects of unstressing on increasing the Ox-U-P appear to be more typical of a gradual reversion to wild-type. The opposite effect with the C-U-P, however, may further indicate the complexity of the nematode-host-nematicide interaction. Specificity of the interactions is hinted at strongly in both cases, since only certain nematode stages are observed to change in the percent extracted from bean roots. While the lower populations (Fig. 1) in the Ox-S-P stages may in part reflect a reduced ability to invade roots (as indicated by the low percentage of J 2, J 3 and adult stages extracted from bean roots; Tab. 5), the lower population levels of the C-U-P (Fig. 1) may be more closely related to other physiologically based factors such as reduced fecundity (as indicated by the similarities in percent of nematodes extracted from roots; Tab. 5).

Conclusive statements

It appears that releasing the C-S-P and Ox-S-P from subnematicidal stressing changes the characters of those populations. While unstressing causes a reduction in the C-U-P, the population levels of the Ox-U-P are increased. The increase in the Ox-U-P appears to be partly attributable to an increased ability to invade the

root system. The decrease in the C-U-P appears to be related to more complex physiologically based factors such as reduced fecundity.

The specific behaviors of all stressed and unstressed populations are strongly influenced by the specific interactions between the nematode-host-nematicide. Behavioral changes even at the level of specific nematode stages attests to the specificity of these interactions.

A very important practical consideration for agriculture may lie in the area of crop rotations or alternate cropping. Stressed and resistant populations of *P. vulnus* were found to reach significantly higher population levels than the W-P on grapevines (Yamashita, Viglierchio & Schmitt, 1985). When stressed, unstressed and wild populations were cultured on Kentucky Wonder beans, however, the W-P reached population levels that were more than five times the levels reached by other populations. While the W-P seems to retain a greater capacity to adapt to new hosts, the specific selection process seems to have narrowed this capacity in both stressed and unstressed populations. Furthermore, removal of the C-S-P from carbofuran stressing appears to remove an element necessary for its normal growth. A grower, who has treated a high money crop with nonfumigant nematicides, may suddenly switch to a crop for which nematode control is economically unfeasible. Even though the crop selected is susceptible to the same nematode species parasitizing the former crop, the grower may be able to avoid economic losses. This depends on the specific host, nematode species and previously applied nematicides. Increasing costs in agriculture and greater demands on ecological safety will demand more accurate pest management programs. In this regard, studies covered here warrant further investigations.

REFERENCES

CHITAMBAR, J. (1983). *The life history and morphology of* Pratylenchus vulnus. Portion Ph. D. Dissert., Univ., California, Davis.

DOLLIVER, J. S. (1961). Population levels of *Pratylenchus penetrans* as influenced by treatments affecting dry weight of Wando pea plants. *Phytopathology*, 51 : 364-361.

EDMUNDS, J. E. & MAI, W. F. (1966). Population increase of *Pratylenchus penetrans* in alfalfa and celery roots infected with *Trichoderma viride*. *Phytopathology*, 56 : 1320-1321.

FRANCO, C. & DURAN, N. (1981). Metabolites of carbofuran : effect on indole-3-acetic acid degradation. *Pesticide Biochem. Physiol.*, 16 : 136-140.

GIEBEL, J. (1979). Biochemical mechanisms of plant resistance to nematodes. *Prace Naukowe Instytutu Ochrony Roslin, Poznan*, 21 : 189-212.

JENSEN, H. J. (1953). Experimental greenhouse host range studies of two root-lesion nematodes, *Pratylenchus vulnus* and *Pratylenchus penetrans*. *Pl. Dis. Reptr*, 384-387.

JONES, A. S. (1976). Metabolism of aldicarb by five soil fungi. *J. Agric. Food Chem.*, 24 : 115-118.

KAPLAN, D. T. & EDWARDS, D. F. (1982). Pesticide/microbe interaction effects on persistence of pesticides in soil. *Vth Intern. Congr. Pesticide Chemistry (IUPAC), Aug. 29-Sept. 4, 1982, Hyoto, Japan.*

KAPLAN, D. T. & KEEN, N. T. (1980). Mechanisms conferring plant incompatibility to nematodes. *Revue Nématol.*, 1 : 123-134.

MARBAN-MENDOZA, N. & VIGLIERCHIO, D. R. (1980). Behavioral effects of carbofuran and phenamiphos on *Pratylenchus vulnus*. III. Penetration and development. *J. Nematol.*, 12 : 119-129.

MATHUR, S. P., HAMILTON, H. A. & VRAIN, T. C. (1980). Influence of some field-applied nematicides on microflora and mineral nutrients in organic soil. *J. Environm. Sci. Health*, 15 : 61-76.

MILNE, D. L., VAN LELYVELD, L. J. & VILLIERS, E. A. (1977). The response of peroxidase and indoleacetic acid oxidase in pineapple roots to foliar applications of phenamiphos. *Agrochemophysica*, 9 : 65-69.

MOUTAIN, W. B. & MCKEEN, C. D. (1962). Effect of *Verticillium dahliae* on the population of *Pratylenchus penetrans*. *Nematologica*, 1 : 261-266.

PATTERSON, M. T. & BERGESON, G. B. (1967). Influence of temperature photoperiod, and nutrition on reproduction, male-female-juvenile ratio, and root to soil migration of *Pratylenchus penetrans*. *Pl. Dis. Reptr*, 51 : 78-82.

ROMAN, J. & TRIANTAPHYLLOU, A. C. (1969). Gametogenesis and reproduction of seven species of *Pratylenchus*. *J. Nematol.*, 1 : 357-362.

SARAH, J. L. (1981). Utilisation de nématicides endothérapiques dans la lutte contre *Pratylenchus brachyurus* (Godfrey) (Nematoda : Pratylenchidae) en culture d'ananas. III. Effets secondaires d'applications foliaires sur la réponse au traitement d'induction florale et sur la floraison. *Fruits*, 35 : 491-500.

STEIFERT, J. & DAVIDEK, J. (1978). The carbamoylation and spontaneous reactivation of the cabbage carboxylesterase after interaction with carbofuran. *Pesticide Biochem. Physiol.*, 8 : 10-14.

WELLING, W. (1977). Dynamic aspects of insect-insecticide interactions. *Ann. Rev. Entomol.*, 22 : 53-78.

YAMASHITA, T. T. & VIGLIERCHIO, D. R. (1986). Variations in

the stability of behavioral changes in nonfumigant nematicide-stressed populations of *Xiphinema index* following release from subnematicidal stress. *Revue Nématol.*, 9 (in press).

YAMASHITA, T. T., VIGLIERCHIO, D. R. & SCHMITT, R. V. (in press). Responses of nematodes to nematicidal applications following extended exposures to subnematicidal stress. *Revue Nématol.*, 9 : 46-60.

ZINOV'EVA, S. V., KOSTYUK, N. A., TURLYGINA, E. S. & SHUBINA, L. V. (1978). [The role of mineral fertilizers in the resistance of plants to nematode infections.] *Trudy Gel'mintologicheskoi Laboratorii (Nematody i akantotsefaly, morfologiya, sistematika, ékologiya i fiziologiya)* 28 (1978) : 67-78.