

Population Characteristics and Dosage Trajectory Analysis for *Mesocriconema xenoplax* in California *Prunus* Orchards

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Abstract: The *Mesocriconema xenoplax* population increased exponentially in a newly planted peach orchard. The rate of increase was greater on Nemaguard than on Lovell rootstock and was reduced by postplant nematicides. Population levels were more stable in an established almond orchard on Nemaguard rootstock. All life stages of the nematode were present year round; lower ratios of juveniles to adults in summer suggested adverse effects of temperature and dry soil. Also in summer, there was a smaller proportion of the population in the upper 30 cm of soil than at greater depths. Nematode dosage, average nematode density multiplied by accumulated degree-days (physiological time) of the sampling interval, was useful in quantifying nematode stress on trees and as an indicator of the nematode management effectiveness. The annual trajectory of the nematode dosage could be determined by two samplings, one in spring and one in fall. A nematode predator, the parasitic fungus *Hirsutella rhossiliensis*, did not regulate ring nematode populations in the newly planted orchard; a recovery period was necessary for increase in the prevalence of parasitism.

Key words: bacterial canker, *Mesocriconema xenoplax*, nematicides, nematode management, population regulation, *Prunus*, rootstocks, stress dosage.

The ring nematode, *Mesocriconema (Criconemella) xenoplax*, predisposes *Prunus* spp. to bacterial canker (BC) caused by *Pseudomonas syringae* pv. *syringae* and contributes to tree decline and mortality in the San Joaquin Valley of California (English et al., 1980; Lownsbery et al., 1973). Bacterial canker is more severe where population densities of *M. xenoplax* reach high levels (Lownsbery et al., 1977). The nematode is involved in a similar complex with *P. syringae* and cold injury in the southeastern United States in a condition known as peach tree short life (PTSL) (Nyczepir, 1990; Nyczepir et al. 1983; Okie et al., 1985). In Michigan, however, tree decline in cherry orchards seems more associated with feeding by the ring nematode than with predisposition (Melakeberhan et al., 1994, 2000).

Most *Prunus* rootstocks support populations of *M. xenoplax* but differ in their host status. For example, Nemaguard rootstock, selected for resistance to *Meloidogyne* spp., is a better host of the ring nematode than the *Meloidogyne*-susceptible Lovell rootstock (Ritchie and Clayton, 1981; Zehr et al., 1976). The incidence of PTSL was also reported greater for trees on Nemaguard than on Lovell rootstock (Nyczepir, 1990). Lovell has been described as partially tolerant to *M. xenoplax* (Nyczepir, 1991; Zehr et al., 1976). Lownsbery et al. (1977) found that scions on both rootstocks succumbed to BC in container experiments and indicated the need for comparisons of the two rootstocks in the field. While Okie et al. (1987) found fewer *M. xenoplax* in pots planted with Lovell than with Nemaguard rootstock, the numbers of nematodes per gram root were

similar. Additionally, certain scions appear to be more susceptible to BC regardless of the rootstock on which they are grafted (Cameron, 1971; Ritchie and Clayton, 1981; Weaver et al., 1979; Zehr et al., 1976).

Preplant and postplant nematicides have been important for management of BC and PTSL. Historically, the postplant nematicide of choice was 1,2-dibromo-3-chloropropane (DBCP) but, following withdrawal of that chemical from the market, there have been some successes with phenamiphos (Nemacur 3; Bayer CropScience, Kansas City, MO). In North Carolina, annual fall applications of phenamiphos reduced ring nematode populations and tree death due to *P. syringae* (Ritchie, 1984, 1989; Ritchie and Clayton, 1981). Nematicides have been more effective in reducing PTSL in orchards on Nemaguard rootstock than on the more tolerant Lovell rootstock (Zehr et al., 1976).

There have been interesting quantitative studies on the effect of rootstocks on the population dynamics of *M. xenoplax*. Degree-day requirements for population doubling were similar for Halford, Lovell, and Nemaguard rootstocks (Wescott and Zehr, 1991). However, quantitative relationships between nematode densities and tree yield or mortality have not been developed. Such relationships are difficult to quantify in perennial trees and vines; they are confounded by annual growth cycles, complex plant phenology, and the previous growth and stress history of the orchard. Additionally, there may be genetic variability within some rootstock species.

Ring nematodes are affected adversely by high mid-summer soil temperature (Lownsbery, 1959). Further, as individuals pass through the lifecycle at rates affected by environmental conditions, the stage structure of the population is potentially in constant flux. How do all these factors affect the potential damage to trees in relation to the structure, abundance, and activity of the population at any point in time? Noling and Ferris (1987) approached the problem of damage functions for a perennial crop, alfalfa, by using a multiple-

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point model that relates crop loss to the rate of increase of nematode dosage. Nematode dosage combines nematode abundance and elapsed degree-days. The concept is similar to the cumulative nematode density assessment used by Ritchie (1988) in that it recognizes the incremental effects of maintained stress; it differs in that it also includes a physiological time component.

The parasitic fungus, *Hirsutella rhossiliensis*, is a specialist predator of nematodes (Jaffee and Zehr, 1985). It is distributed widely in California peach and almond orchards, and large numbers of parasitized *M. xenoplax* are sometimes observed (Jaffee et al., 1988). The fungus has been described as a weak regulator of *M. xenoplax* population (Jaffee et al., 1989).

The studies reported herein were designed to measure the impact of management on the trajectory of the nematode dosage and any relationship between the dosage and tree yield or mortality. Specific objectives were to: (i) determine population development of *M. xenoplax* on Lovell and Nemaguard rootstocks under field conditions; (ii) quantify the relationship between nematode dosage and yield loss or tree mortality; (iii) examine the age structure of *M. xenoplax* populations through time; (iv) examine the relationship between predation of *M. xenoplax* by *H. rhossiliensis* and the product of nematode densities and time; and (v) provide a framework for decisions based on management costs, management effectiveness, and rate of increase of nematode dosage.

MATERIALS AND METHODS

Field studies were conducted at sites in Stanislaus and Merced counties, California. Both sites were in areas with high incidence of BC.

Livingston Site (Merced County): The site was a 6.3-ha orchard with soil texture ranging from loamy sand to sand. In most of the field, there were no discernible differences in soil texture within the upper 1.5 m of the soil profile. In the upper 75 cm, sand content ranged from 79% to 86% and clay from 9% to 12%; in the second 75 cm, sand ranged from 69% to 84% and clay from 8% to 18%. In the southwest corner of the field (designated as replicate 7), clay content was slightly greater (16% to 18%) in the deeper 75 cm of the soil profile. The orchard site had a 20-year history of Faye Elberta peach on S-37 rootstock. The previous orchard was removed in the late summer, and 1,3-dichloropropene (Telone II; Dow AgroSciences, Indianapolis, IN) fumigant nematicide was applied in November in 3.5-m-wide tree-row strips. The fumigant was applied by a commercial applicator at label rates. The new orchard was established the following March. The soil in a 3-m strip along the tree row was not tilled, and weeds in that strip were controlled by herbicides. Between the undisturbed strips, weeds were controlled by shallow tillage. All cultural and pest management practices conformed

to recommendations for non-bearing and bearing trees within that region (LaRue and Johnson, 1989).

The orchard was designed to test the performance of two rootstocks with a common scion, Halford peach. The rootstocks were Lovell and Nemaguard, planted in alternating four-row strips. The field was drip-irrigated and had, on selected rows, valves that could be closed while nematicides were applied through the drip system. In a randomized complete block design, eight replicates of experimental plots were designated across the field; each consisted of four neighboring rows of trees with 20 trees in each of the rows. The neighboring rows of each replicate represented separate treatments: Nemaguard and Lovell rootstocks, with and without drip-irrigation-applied nematicide.

During year 1, oxamyl (Vydate Dupont, Wilmington, DE) was applied at 1.1 kg a.i./ha in the nematicide treated rows in March, April, May, June, and July. During year 2, phenamiphos was applied at 5.6 kg a.i./ha in April and October. In the third and subsequent years, the same rate of phenamiphos was applied only in October. Nitrogen in the form of UAN-32, a solution of NH_4NO_3 and urea, was applied through the drip system, at the discretion of the orchard manager, to all tree rows as follows: 11.2 kg N/ha in April and September of year 1, 17.9 kg N/ha in April of year 2, 54.9 kg N/ha in October of year 3, 22.4 kg N/ha in both April and May of year 4.

Escalon Site (Stanislaus County): The site was a 2.4-ha orchard divided by berms into four 0.6-ha irrigation basins. Each basin was flood-irrigated from a pipeline running down the center of the orchard. The soil was a deep sand of high porosity and rapid drainage, with low organic matter (<1%). This site had a history of almond production. The preceding crop, an almond orchard on Lovell rootstock, was declining in production after 20 years. Five years before the start of this study, the previous orchard was removed, the site treated at label rates with 1,3-dichloropropene soil fumigant, and a new orchard of almonds (Nonpareil, Peerless and Mission scions on Nemaguard rootstock) was planted with approximately 140 trees in each basin. Cultural practices in the orchard conformed to recommendations for the region (University of California Integrated Pest Management, 2002). Establishment of the newly planted trees was poor; each year up to 10% of the trees succumbed to BC. Soil was excavated from each dead tree site to a depth of 180 cm, roots were removed, and the soil returned to the hole. Each site was treated with 0.45 kg of methyl bromide introduced 60 cm below the soil surface. The tree sites were replanted with almond trees on Nemaguard rootstock. Consequently, at the initiation of our study, trees in the orchard were 1, 2, 3, 4, and 5 years old. Older trees seemed more tolerant of BC; usually it was the younger trees that died.

Constrained by the layout of the orchard and design of the irrigation system, we tested summer and fall ap-

plications of phenamiphos in an attempt to reduce the annual tree mortality due to BC. One flood basin received 10 kg/ha phenamiphos each July and October (Treatment A), the second received a single application of 20 kg/ha in October of the first year of the study and none thereafter (Treatment C). The third received 20 kg/ha in July initially and 10 kg/ha in October of the next year and each year thereafter (Treatment D), and the fourth was an untreated control (Treatment B). Although there was replication of observations within treatments, it was not possible to replicate the treatments, because of the flood-basin design of the field.

Nematode sampling and extraction: At the Livingston site, populations of *M. xenoplax* were undetectable at planting (March). Population densities and stage structure profiles of the nematode were assessed in all plots at monthly intervals from August of year 1 through October of year 2, at 2 month intervals from then to December of year 4, a single sampling in June of year 5, samplings in February and September of year 6, and a final sampling in May of year 7. At each date, soil samples were taken from five trees selected at random throughout the 20-tree row of each plot. Two soil cores were taken to a depth of 60 cm with a 5-cm-diam. auger, one from each side of each tree, in the tree row and within 30 cm of the drip emitter closest to the edge of the tree canopy. This provided 10 cores/plot, which were composited, mixed, and subsampled for nematode extraction.

At the Escalon site, soil samples were taken at approximately monthly intervals from August of year 1 through October of year 2 and then at 3-month intervals through April of year 4. Samples were taken at the drip line on the east side of each tree. In one block, samples were taken also on the north, south, and west sides during a portion of the sampling period to determine any effects of cultivation or traffic pattern. Samples were taken with a 5-cm-diam. auger at 30-cm depth intervals to a depth of 90 cm from six trees, selected at random in each block but only from the trees that were 5 years old at the start of the study.

Nematodes were extracted from 600 cm³ subsamples of each sample using elutriation and sugar (425 g/L) centrifugation to enhance recovery of *M. xenoplax* (Byrd et al., 1976; Jaffee et al., 1989; Jenkins, 1964). Extraction efficiency of the sugar centrifugation process for each life stage of *M. xenoplax* was determined by seeding soil with known numbers of each life stage and assessing recovery by this technique. An ocular grid was calibrated in relation to the dimensions of J2, J3, J4, and adult nematodes for rapid classification. Numbers of each life stage were counted in the samples and corrected for extraction efficiency (0.44, 0.47, 0.51, and 0.69 for J2, J3, J4, and adults, respectively).

Fungal antagonists of ring nematode: Parasitism of *M. xenoplax* by *H. rhossiliensis* was quantified at the Living-

ston site. Nematodes extracted from each sample were treated with 0.5% NaOCl, rinsed, and suspended in 10 ml water. Aliquots (333 µl) were spread on water agar amended with 200 parts 10⁻⁶ streptomycin sulfate and incubated at 22 °C for 5 days. Plates were assessed to determine the number of cadavers from which *H. rhossiliensis* hyphae emerged (Jaffee et al., 1988, 1989). Incidence of parasitism was calculated as the percentage of samples in which any parasitism was observed; prevalence of parasitism was calculated as the percentage of individuals in a sample that were parasitized.

Tree damage, orchard performance, and bacterial canker: Tree growth and vigor were measured annually at the Livingston site. The measurements included leaf weights (five leaves from each of 5 trees/plot), shoot lengths, visual tree vigor ratings (subjective to 1-to-3 scale), trunk diameters, photosynthesis rates (Li-Cor 6000 IR CO₂ gas analyzer, Li-Cor, Lincoln, NE), and yield of peaches. Incidence of BC and tree mortality were assessed annually at both sites.

Data analyses: In annual crops, the time frame is sufficiently short, and the initial population sufficiently synchronous, that critical-point predictive models of crop loss or population dynamics can be based on the nematode population level at a single point in time. In perennial crops, where abundance and characteristics of nematode populations, and the size and vigor of their host, vary within and across years, repeated assessments of the population may be necessary (Ferris and Noling, 1987; James, 1974). One approach to assessing the damage potential of nematodes in perennial crops is to measure, cumulatively, the nematode dosage as the concentration of nematodes present multiplied by the time interval. The population is measured at multiple points in time to allow development of a multiple-point model (Ferris and Noling, 1987; Noling and Ferris, 1987). The concentration for a given interval is the average population density during that interval. As subsequent time intervals are included in the sampling program, the trajectory of the nematode dosage can be determined. A refinement of this approach is to consider the effects of temperature on nematode activity by measuring time in degree-days, effectively creating a physiological time scale for the interaction of nematode and host. In this study, we measured the nematode dosage through time as the cumulative product of average nematode density and degree-days using daily soil temperature data at 15-cm depth (University of California Integrated Pest Management, 2003).

Because the irrigation basin layout at the Escalon plot did not allow a replicated experimental design of the nematicide treatments, nematode dosage data for individual treatments at that site are presented as a test of the concept and are not subjected to statistical analysis. However, replicated observations within treatments across time on nematode dynamics and population structure are comparable. The depth distribution of *M.*

xenoplax was determined from the 30-cm depth increment samples. Mean population densities at each depth were calculated as the average of the four samples at that depth from each tree.

Theory and experiment in population regulation suggest that when specialist predators are under equilibrium conditions with their prey and are exerting a regulatory effect, there is a strong relationship between the probability of predation and the abundance of the prey (Turchin, 1995). However, the predator-prey system (*H. rhossiliensis*-*M. xenoplax*) in the Livingston field during the sampling period was not under equilibrium conditions; it was recovering from major disturbance. We used the nematode dosage in the relationship between predator and prey as a means of introducing a time element that would accommodate the non-equilibrium state of the system. To avoid the cause-and-effect implication of the term dosage, we use "area under the nematode density curve" (AUNDC) as a descriptor of the independent variable in this instance. By regression analysis, we determined the relationships of prevalence and incidence of parasitism by *H. rhossiliensis* to the AUNDC.

RESULTS

Population increase and seasonal cycles: At the Livingston site, starting from undetectable levels at the March planting date, population densities of *M. xenoplax* developed rapidly on the untreated Nemaguard rootstock (Fig. 1A). They reached 28,000 individuals/L soil by day 546 (August of year 2). They remained at or near that level until day 914 (September of year 3). Population densities on the untreated Lovell rootstock developed at a slower rate (Fig. 1B) and reached a maximum by day 768 (April of year 3). Soil in the orchard was extremely dry from September through November of year 3, preceding winter rain, and there was an application of an unusually high level of UAN-32 (54.9 kg N/ha) to the whole field in October. Population levels of *M. xenoplax* decreased in all treatments by day 977 (November of year 3). The population recovered in year 4 but not to the levels achieved in the summer of year 3. Thereafter (years 5 and 6) population levels stabilized below 10,000/L soil on both rootstocks.

Oxamyl applications in the spring and summer of year 1, and phenamiphos applications in the spring and fall of year 2, maintained population levels at less than half of those in the untreated rows for each rootstock (Fig. 1A,B). In year 3 and beyond, when phenamiphos was applied only in the fall, the nematode population was affected less than in previous years and population densities were similar whether or not the nematicide was applied.

At the Escalon site, sampling commenced in August of year 1. Treatment effects on *M. xenoplax* populations were not distinguishable among the four plots until

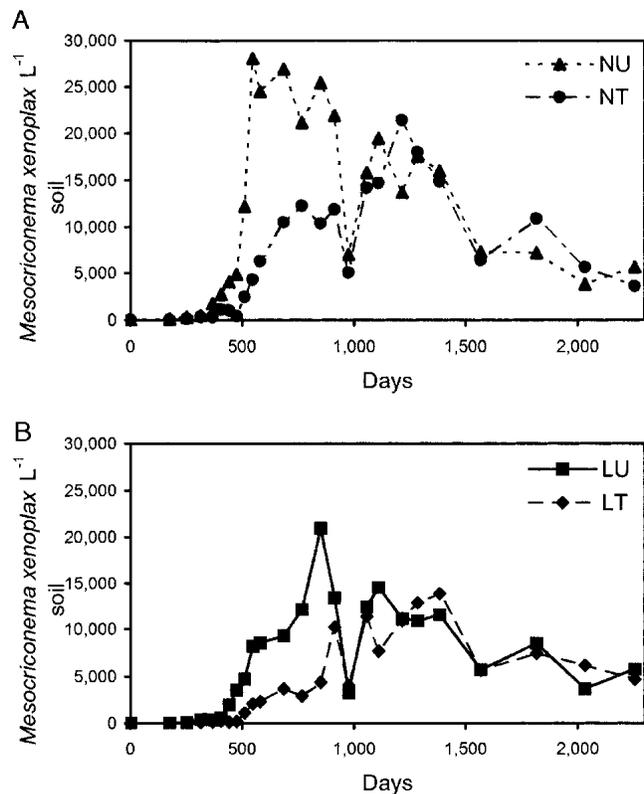


FIG. 1. Livingston site: Mean abundance of *Mesocriconeema xenoplax* in a peach orchard on Nemaguard (N) and Lovell (L) rootstocks, treated (T) and untreated (U) with oxamyl (1.1 kg a.i./ha in the nematicide treated rows in March, April, May, June, and July of year 1) and phenamiphos (5.6 kg a.i./ha in April and October of year 2; 5.6 kg a.i./ha in October of years 2–6) as postplant nematicides. For ease of interpretation of temporal scale, Day 0 = March 1 of year 1 (planting date), Day 500 = July 14 of year 2, Day 1000 = November 26 of year 3, Day 1500 = May 15 of year 5, Day 2000 = August 22 of year 6.

after day 526 (January of year 3) (Fig. 2). In the final 15 months, population levels were greatest in Treatment C, which received a single application of phenamiphos in the fall of the first year (day 30) and none thereafter. By the final sampling (day 979, April of year 4), population levels in Treatment A (initial summer application followed by applications each fall) had also increased substantially (Fig. 2).

Age structure and spatial patterns: All vermiform life stages of *M. xenoplax* were present year round at both sites (Fig. 3). In addition, at both sites, the proportion of J2 was greatest in the spring (March, April), lowest in the summer (July, August), and increasing in the fall (October). The relative abundance of other life stages remained stable throughout the year. Proportionally fewer *M. xenoplax* were present in the upper 30 cm of soil during the summer months than during the balance of the year at the Escalon sites (Fig. 4A). The proportional distribution of all life stages, including adults, was greater deeper in the soil (30–90 cm) during the summer (Fig. 4A,B). There were fewer J2 present per adult during the summer months at all depths, and

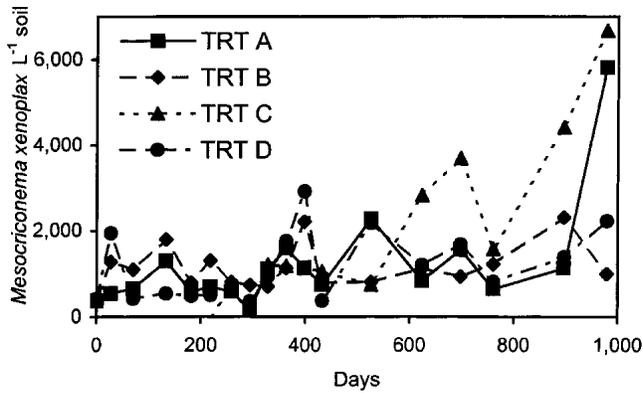


FIG. 2. Escalon site: Abundance of *Mesocriconema xenoplax* in an almond orchard on Nemaguard rootstock treated with 10 kg/ha phenamiphos each July and October (A), a single application of 20 kg/ha in October of the first year and none thereafter (C), 20 kg/ha in July initially and 10 kg/ha in October of the next year and each October thereafter (D), and an untreated control (B). For ease of interpretation of temporal scale, Day 0 = August 1 of year 1, Day 500 = December 26 of year 2, Day 1000 = April 29 of year 4.

this trend was particularly evident in the top 30 cm of soil (Fig. 4C).

The orchard floor at the Escalon site was maintained flat throughout the year to allow flood irrigation and for ease of harvesting. Although the tree spacing was greater in an east-west direction and there was more traffic on those sides of the trees, there were no differences in population levels of *M. xenoplax* between the north/south sides and east/west sides of the trees (data not shown).

Fungal antagonist response: The incidence of *H. rhossiliensis* in soil samples from the Livingston orchard

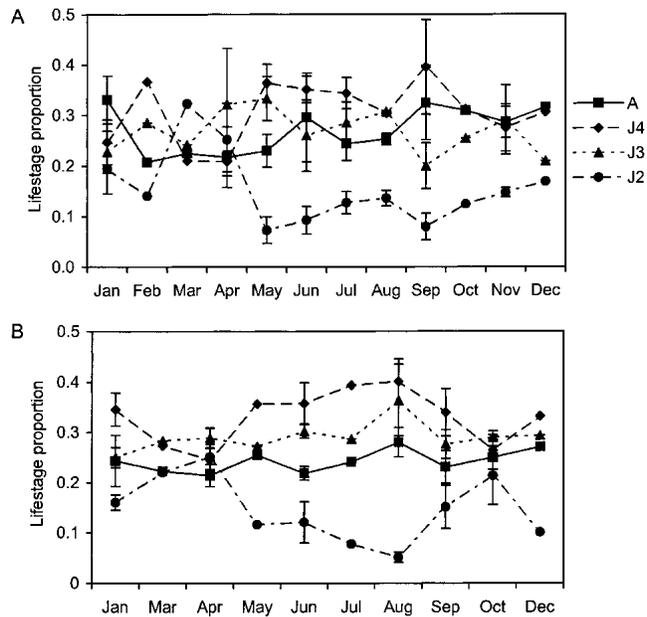


FIG. 3. Annual proportional lifestage distribution of adult and juvenile stages (J2 through J4) of *Mesocriconema xenoplax* in a peach orchard at the Livingston site (A) and an almond orchard at the Escalon site (B). Data averaged across years, rootstocks and nematicide treatments; bars are ± 1 s.d.

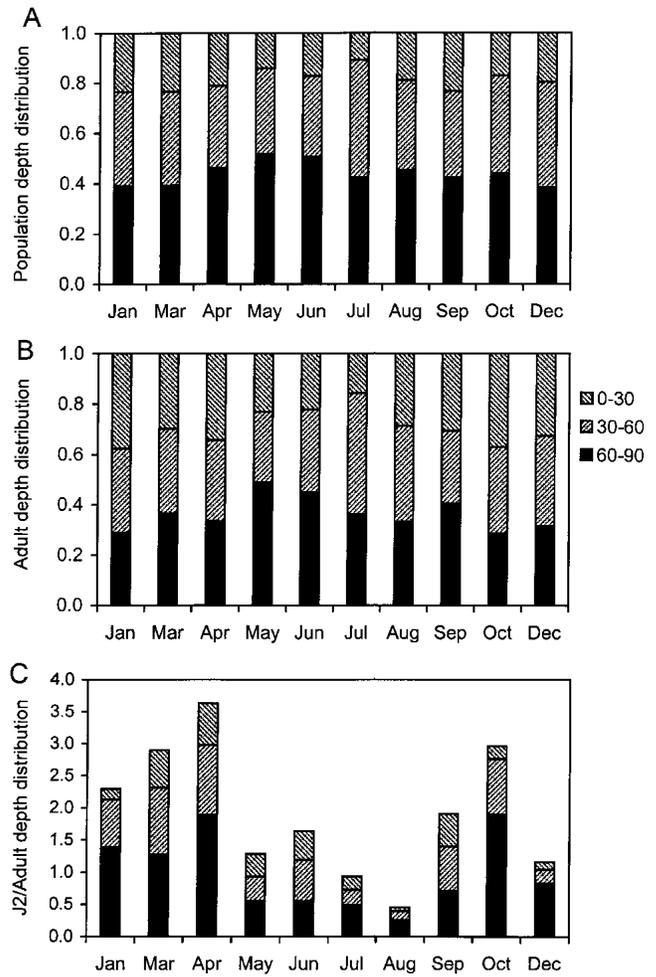


FIG. 4. Annual depth distribution (0–30, 30–60, and 60–90 cm) of *Mesocriconema xenoplax* in an almond orchard at the Escalon site. A) Proportional depth distribution of the whole population. B) Proportional depth distribution of adults. C) Ratio of second-stage juveniles (J2) to adults with depth, as an indicator of population productivity. Bars are stacked in each panel.

(that, is the percentage of samples in which at least one nematode was parasitized by the fungus) increased linearly with AUNDC (Fig. 5A). Similarly, AUNDC was a good measure of the percentage of all nematodes in a sample that were parasitized (that is, the prevalence of parasitism) (Fig. 5B). The relationship between prevalence of parasitism of *M. xenoplax* and the AUNDC differed between plots that did not receive postplant nematicide and those that did. Where phenamiphos was applied either once or twice a year, the prevalence of parasitism of *M. xenoplax* by *H. rhossiliensis* increased at a slower rate in relation to AUNDC than in plots that did not receive nematicide (Fig. 5C).

Damage trajectories and treatment effects: At the Livingston site, the rate of increase in nematode dosage was greater in Nemaguard plots than Lovell plots if nematicides were not applied. The spring and fall nematicide applications in years 2 and 3 reduced the rate of increase in nematode dosage on the respective

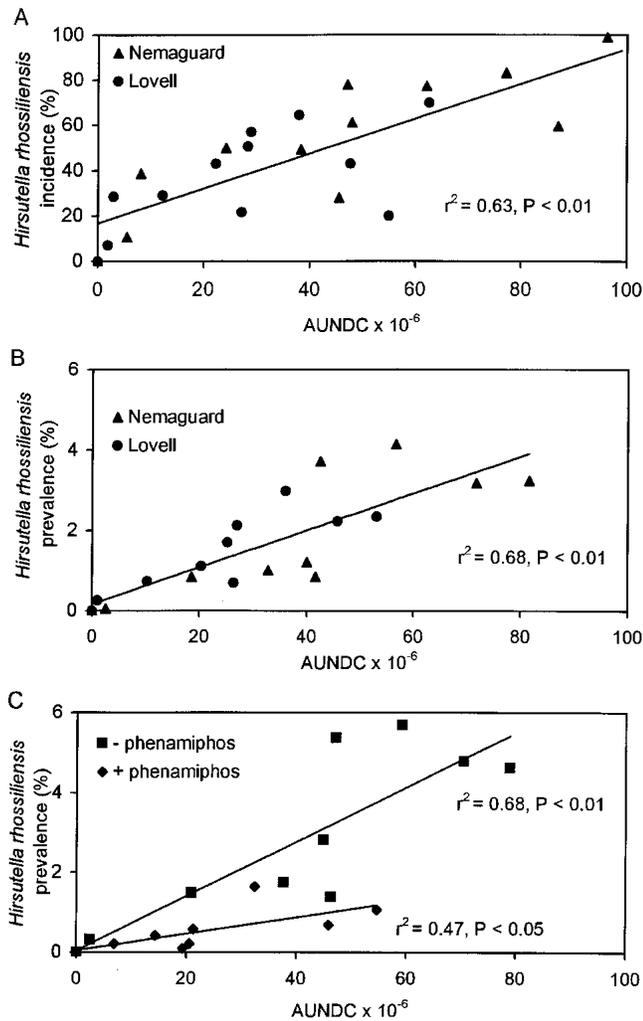


FIG. 5. Relationship between predation of *Mesocriconeema xenoplax* by *Hirsutella rhossiliensis* and the area under the nematode density curve (AUNDC) in samples from peach trees on Lovell and Nemaguard rootstock at the Livingston site. A) Incidence of *H. rhossiliensis* parasitism (percentage of samples in which some parasitism occurred). B) Prevalence of *H. rhossiliensis* parasitism (percentage of individuals parasitized). C) Effect of phenamiphos on prevalence of *H. rhossiliensis* parasitism, averaged across rootstocks.

rootstocks (Fig. 6A,B). Spring and fall nematicide treatment in plots of each rootstock reduced the nematode dosage by about 70% in each case; however, the application of nematicide only during fall in year 4 was apparently ineffective in moderating the trajectory of the nematode dosage (Fig. 6C). Nematode populations were not uniformly distributed throughout the orchard. When the eight treatment replications were stratified into regions of low nematode density (stratum 1, replicates 1 to 6) and high nematode density (stratum 2, replicates 7,8), nematode dosage increased at a greater rate in stratum 2 than in stratum 1 in plots not treated with nematicide (Fig. 7A,B). The strata also correlated with tree performance and slight differences in soil texture. Interestingly, dosage trajectories on Nemaguard and Lovell rootstock in plots not receiving nematicide were indistinguishable in the high-density

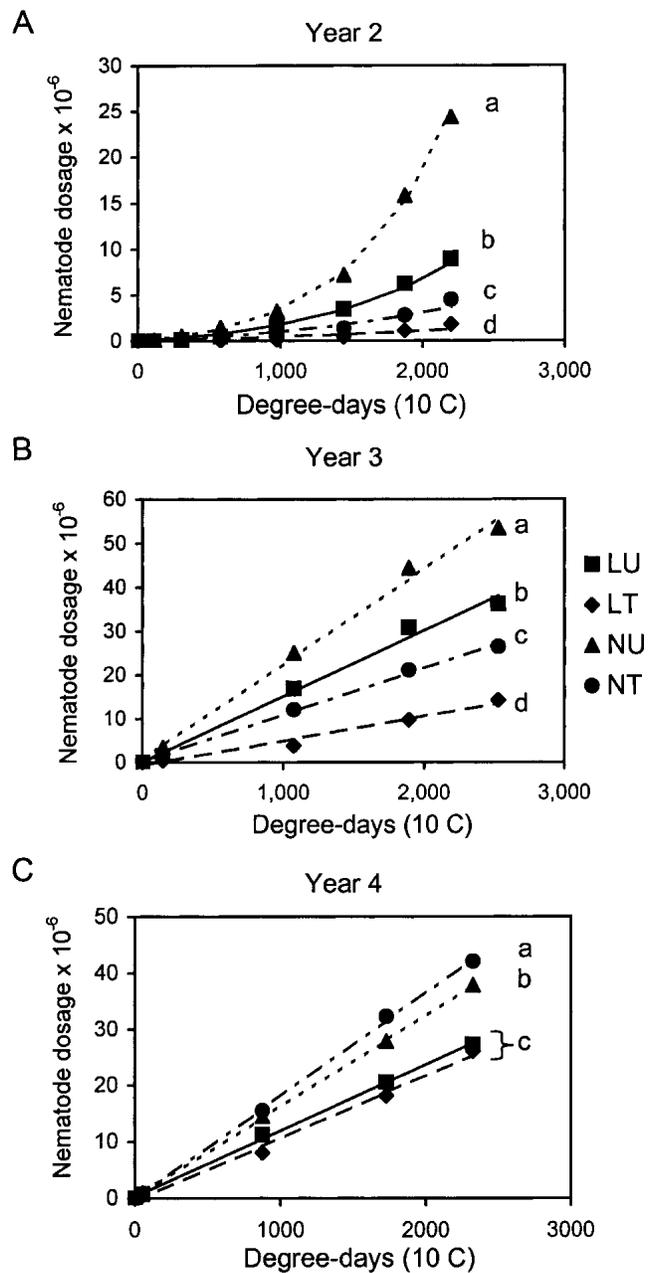


FIG. 6. Three-year annual trajectories of cumulative nematode dosage (average population density multiplied by the physiological time interval [DD_{10C}] between consecutive sampling periods) for *Mesocriconeema xenoplax* in a peach orchard on Nemaguard (N) and Lovell (L) rootstocks, treated (T) and untreated (U) with postplant nematicides, at the Livingston site. Slopes of lines marked with different lowercase letters differ, $P < 0.05$.

stratum in year 3. Again, the fall-only nematicide treatment in year 4 was ineffective (Fig. 7E,F).

At the flood-irrigated Escalon site, roots were less concentrated than at the drip-irrigated Livingston site, and population densities of *M. xenoplax* were lower. Although statistical analysis of these data is not appropriate, dosage trajectories for different treatments are presented. During year 3, the rate of increase of the nematode dosage in Treatment C (single application of 20 kg/ha phenamiphos in the fall of year 1 and none

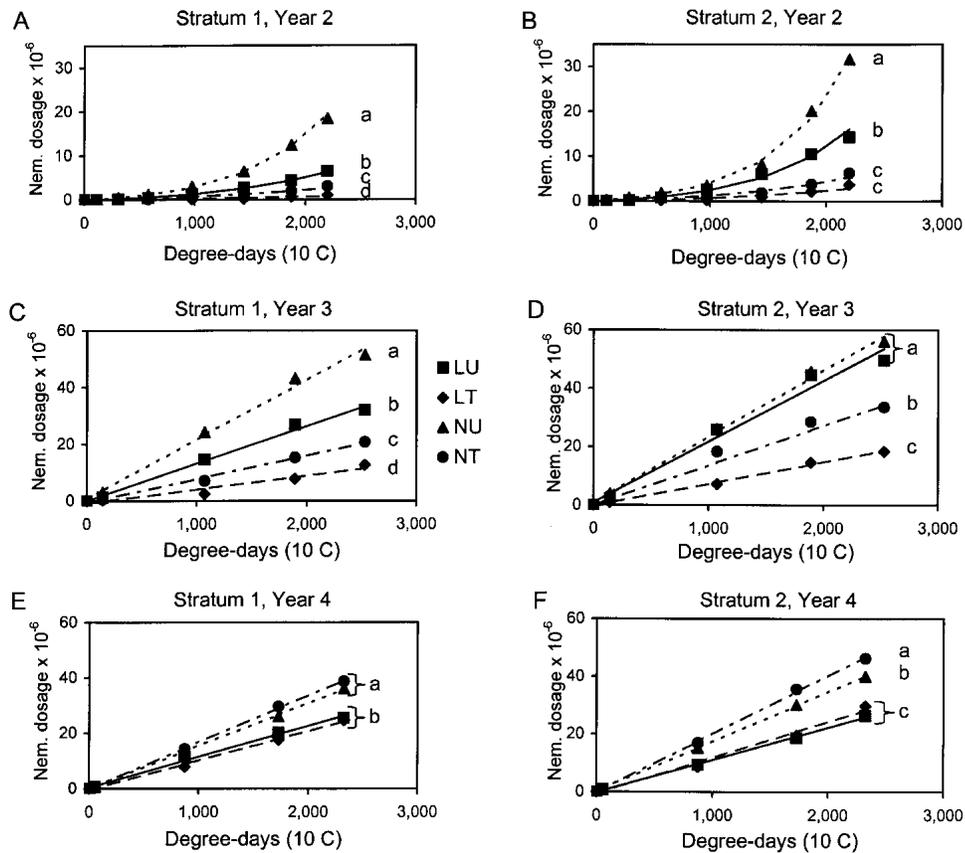


FIG. 7. Three-year annual trajectories of cumulative nematode dosage (average population density multiplied by the physiological time interval [DD_{10C}] between consecutive sampling periods) for *Mesocriconema xenoplax* in two strata of a peach orchard on Nemaguard (N) and Lovell (L) rootstocks, treated (T) and untreated (U) with postplant nematicides, at the Livingston site. Stratum 1 (replicates 1-6) had lower nematode densities, and stratum 2 (replicates 7,8) had higher nematode densities. Slopes of lines marked with different lowercase letters differ, $P < 0.05$.

thereafter) was particularly dramatic (Fig. 8). The rate of increase in dosage in Treatment D (20 kg/ha in the summer of year 1 and 10 kg/ha in the fall of year 2 and each fall thereafter) was never different qualitatively from that in the untreated control (Treatment B). By contrast, the trajectory of the nematode dosage appeared lower during year 1 but not thereafter in Treatment A (10 kg/ha phenamiphos each summer and fall).

Tree damage and orchard performance: Peach yield was unaffected by rootstock or nematicide in 3 individual years or cumulatively over the 3-year period (Table 1). Plant-growth measurements generally did not differ between trees on the Nemaguard and Lovell rootstock. Where there were differences in root weight, leaf weight, and plant vigor rating, measurements were greater on the Nemaguard than the Lovell rootstock, generally consistent with experimental comparisons of their growth (Werner and Young, 1982) (Table 1).

At the Livingston site, BC symptoms occurred in several areas of the field, but tree death occurred only in replicate 7 (stratum 2) on Nemaguard rootstock in the presence of high population densities of ring nematode and highest nematode dosage (Fig. 7B,D,F). Symptoms of BC, mainly death of branches, in other parts of

the field were always in Nemaguard plots without nematicide. By year 4, there were three dead trees, no dead scaffold limbs, and two dead branches among the 160 trees on Nemaguard rootstock treated with nematicide. There were four dead trees, four dead scaffold limbs, and 93 dead branches among the 180 trees on Nemaguard rootstock without nematicide. There were no BC symptoms on trees on Lovell rootstock, regardless of nematicide treatment.

Plant growth and almond yield were not measured at the Escalon site. In spring of year 2, there were no symptoms of BC in the plots that received fall applications of phenamiphos (Treatments A and C). However, 8% of the trees died and 4% were infected in the untreated control plot (Treatment B). In Treatment D, which received nematicide in summer but not fall of year 1, 7% of the trees died and a further 7% exhibited BC symptoms.

DISCUSSION

The trajectories of the nematode dosages indicated the effectiveness of nematode management strategies. At the Livingston site, the characteristics of the ring nematode populations, as determined by rootstock and

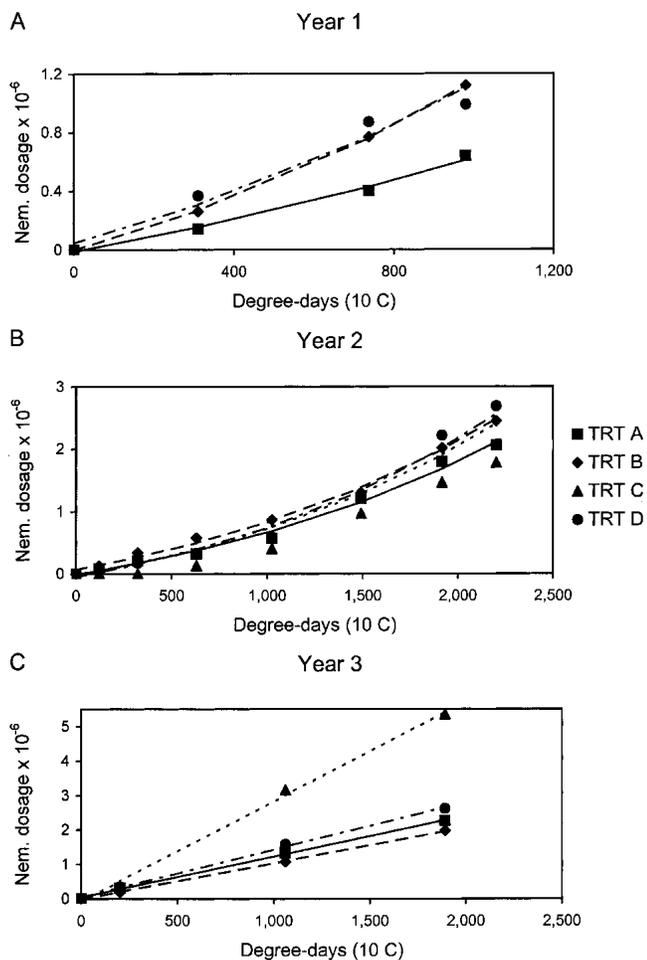


FIG. 8. Three-year annual trajectories of nematode dosage, defined as the cumulative average density multiplied by the physiological time interval (DD_{10C}) between consecutive sampling periods, for *Mesocriconema xenoplax* in an almond orchard on Nemaguard rootstock at the Escalon site. Treatment A = 10 kg/ha phenamiphos each summer and fall; Treatment C = a single application of 20 kg/ha in fall of the first year and none thereafter; Treatment D = 20 kg/ha in summer initially and 10 kg/ha in fall of the next year and each fall thereafter; Treatment B = untreated control. These data are presented for illustration of concept because the experimental design was constrained by field layout and did not allow rigorous statistical analysis.

nematicide treatments, were evident during the first 3 years of the experiment. Spring and fall nematicide applications to plots of each rootstock reduced the nematode dosage by about 70%. Several nematicides, including phenamiphos, are reported to become less effective when applied repeatedly to soils, possibly due to elevated microbial degradation (Davis et al., 1993; Johnson, 1998). Treatment with phenamiphos in fall of year 3 at Livingston seemed relatively ineffective based on the population levels and nematode dosage trajectories observed in year 4.

For ring nematode control, our studies suggest that the critical application times for phenamiphos are in spring and summer, and that fall applications are less effective. One concern with this conclusion is that our

nematode extraction technique does not require the nematodes to be alive. If nematodes killed by phenamiphos application in fall did not degrade rapidly, they may have been included in our counts. However, we did not see any shift in nematode counts or the dosage trajectory in spring following fall nematicide applications. We infer from these observations that spring and summer applications of phenamiphos are most effective in moderating the rate of increase of *M. xenoplax* dosage. That conclusion agrees with observations from many other orchards (M. V. McKenry) and is consistent with reports from the southeast United States that applications of phenamiphos in spring and fall are more effective in reducing ring nematode populations than applications in fall alone (Ritchie, 1989). We ascribe the dramatic reduction in population levels of *M. xenoplax* in all treatments in November of year 3 at Livingston to the combination of dry soil (Lawrence and Zehr, 1978) and NH_3 release from the unusually high application rate of UAN-32 (Mojtahedi and Lownsbery, 1976).

If nematode dosage trajectories are a useful management tool, what sampling frequency is necessary to detect changes in their slope? In our studies, we measured nematode numbers up to six times per year and used those data to calculate annual and cumulative dosages. We tested the concept by determining whether it was possible to separate treatment effects using nematode dosages calculated from data for a sampling time in spring and one in fall. In each case, an acceptable separation of the dosage trajectory slopes, but with somewhat less precision, could be determined from a biannual sampling (data not shown).

Some data are available on the effect of temperature on life-course events of *M. xenoplax*. Degree-day requirement for egg hatch at temperatures between 10 °C and 30 °C was 154 DD_{9C} (degree-days base 9 °C) (Wescott and Burrows, 1991). In related studies, *M. xenoplax* increase on *Prunus* species was studied under greenhouse conditions to determine the "proportionate doubling increment" (Wescott and Zehr, 1991). Those data allow calculation of a requirement of 481 DD_{9C} , based on air temperatures, for population doubling. Seshadri (1964) determined that the egg stage was completed in 11 to 13 days, the J2 stage in 3 to 5 days, the J3 stage in 4 to 7 days, the J4 stage in 5 to 6 days, and the total life cycle in 25 to 34 days at temperatures of 22 °C to 26 °C. Females produced 4 to 5 eggs/day after a 2 to 3-day preoviposition phase. Using the 9 °C base temperature of Wescott and Burrows (1991), the Seshadri (1964) data allow calculation of life-course duration of approximately 450 DD_{9C} .

At the 15-cm soil depth, the annual DD_{10C} accumulation at both sites was approximately 2,500, which would accommodate ca. 5 generations/year. It is difficult to extrapolate from air temperatures to the temperature of wetting and drying soil. However, if the soil

TABLE 1. Production and vigor ratings for Halford peach on Nemaguard and Lovell rootstocks treated or untreated with postplant nematicide at the Livingston site.

Variable ^a and year	Rootstock		Nematicide		Rootstock and nematicide treatment means			
	Lovell	Nemaguard	Control	Nematicide ^b	Lovell untreated	Lovell treated	Nemaguard untreated	Nemaguard treated
Root wt. y4	16.8	23.2**	18.6	21.8**	15.8	17.7	21.0	25.4
Leaf wt. y2	6.0	6.3	6.6	5.7**	6.4	5.6	6.8	5.8
Leaf wt. y3	5.9	6.3**	6.2	6.1	5.9	5.9	6.5	6.2
Leaf wt. y4	6.6	6.5	6.5	6.6	6.4	6.9	6.7	6.4**
Leaf wt. y2-4	18.5	19.2**	19.3	18.4**	18.6	18.3	19.9	18.5*
Shoot lth. y2	94.3	93.1	93.2	94.0	93.5	95.1	93.0	93.1
Shoot lth. y3	56.1	57.4	54.7	58.8*	52.5	59.6	56.7	58.2
Shoot lth. y4	67.3	64.0	64.8	66.3	67.2	67.4	62.7	65.3
Shoot lth. y2-4	217.7	214.5	212.8	219.2	213.2	222.2	212.4	216.6
Vigor y2	2.4	2.7*	2.5	2.6	2.3	2.6	2.7	2.7
Vigor y3	2.8	2.9	2.9	2.9	2.8	2.9	2.9	2.9
Vigor y4	2.8	2.9*	2.8	2.9*	2.7	2.9	2.9	3.0
Vigor y2-4	8.1	8.5**	8.1	8.5**	7.7	8.4	8.4	8.6
Yield y2	47.4	45.1	51.6	40.8	53.8	41.0	49.6	40.5
Yield y3	55.6	60.4	60.4	55.9	57.2	54.0	63.2	57.6
Yield y4	57.7	53.6	53.5	57.6	55.7	59.7	51.6	55.7
Yield y2-4	160.8	159.1	165.5	154.3	166.7	154.8	164.4	153.8
Photo y2	12.3	13.1	12.5	13.0	12.2	12.4	12.7	13.5
Photo y3	11.5	10.2	10.5	11.0	11.1	11.9	10.0	10.3
Trunk diam y2					5.0	5.3	5.6	6.1
Trunk diam y3					9.0	9.2	9.6	10.1
Trunk diam y4					10.7	11.5	11.3	12.0

Data are means of eight replicates. * indicates differences at the $P = 0.05$ level among means in columns to left, ** indicates that differences are at $P = 0.01$ level. ^a Variables: Root weight (g/1,000 cm³ soil); Leaf weight (g); Shoot length (cm); Visual tree vigor rating (1-3); Trunk diam. (cm); Fruit yield (lb/tree); Photosynthesis rate (mg CO₂/dm²/hr); $y =$ year.

^b In y1, oxamyl was applied at 1.1 kg a.i./ha in March, April, May, June, and July; in y2, phenamiphos was applied at 5.6 kg a.i./ha in April and October; in y3 and subsequent years, 5.6 kg a.i./ha phenamiphos was applied only in October.

temperature was, on average, 5 °C lower than the air temperature, the 481 DD_{9C} air temperature population doubling time (Wescott and Burrows, 1991) would equate to around 350 DD_{10C} soil temperature under our field conditions. Then the population of *M. xenoplax* could have doubled seven times in the course of the 2,500-DD_{10C} year and a starting population of 200 individuals would increase to 26,000 in the course of a year. We saw such increases during the first 500 days at the newly planted and highly disturbed Livingston site. Thereafter the population stabilized, possibly due to limitation of resources, change in growth physiology of the host, and regulatory effects of natural enemies.

All vermiform life stages of *M. xenoplax* were present year round at both sites and at all depths. However, there were some seasonal effects. At the Livingston site, irrigation water was delivered through a drip system at frequent intervals, maintaining a moist zone of soil throughout the year. The Escalon site was irrigated by flooding of large basins when the soil became dry. Consequently, the root-zone soil at that site was subjected to extreme wet and dry cycles, particularly in the upper 30 cm. Soil temperatures at both sites ranged from 10 °C to 30 °C at 15-cm depth (University of California Integrated Pest Management, 2003). However, the favorable temperature range for *M. xenoplax* is 22 °C to 26 °C and reproduction is suppressed at 28 °C (Lownsbery, 1961; Seshadri, 1964), so periods of unfavorable condi-

tions were experienced. Inclusion of an upper threshold for nematode activity is a potential refinement of the model. However, because temperature data were recorded only at 15-cm depth, they do not reflect conditions for all individuals in the population.

Seasonal differences in the relative abundance of J2 in the *M. xenoplax* population may be attributed to an arrested rate of development during the winter months and a flush of hatch of accumulated eggs in spring. The higher soil temperatures of the upper soil layers in summer, coupled with the extreme drying and wetting cycles created by the irrigation strategies at the Escalon site, probably account for the reduced productivity of the population as exhibited by the lower abundance of J2 in relation to adults. These observations substantiate earlier reports that population levels of *M. xenoplax* decrease in summer in California when soil becomes warm and periodically dry (Lownsbery, 1959).

The majority of the *M. xenoplax* population was located at depths greater than 30 cm and, in the summer months when the soil was driest, was at depths greater than 60 cm. That has important implications for assessment of population levels in well-drained soils subject to moisture extremes. Although we do not have depth distribution data for the Livingston site, we expect that the differences would not have been as dramatic as they were at the Escalon site due to the more uniform soil moisture conditions afforded by the drip irrigation.

The lack of difference in nematode abundance at the canopy edge within and between rows suggests that the minimal soil disturbance in the Escalon orchard did not affect root or nematode distribution, even in the upper 30 cm of soil.

Densities of a regulated population have a stationary probability distribution. That condition may have been approached after about day 1500 at the Livingston site and throughout the study at the Escalon site. At an equilibrium state in predator-prey systems, regulation of a prey population by a predator is a function of prey density (Turchin, 1995). Density-dependent predation of *M. xenoplax* by *H. rhossiliensis* has been demonstrated by Jaffee et al. (1989) under the stable conditions of mature peach orchards. At the Livingston site, as is common in agricultural situations, the predator-prey system was not in an equilibrium state initially, i.e., it was recovering from major disturbance. After disturbance, the relative distributions of predator and prey are changed and many prey patches have no predators. With passage of time, more of the prey patches are colonized by the predator and equilibrium can become established.

In the present study, the population of ring nematodes increased exponentially from initially undetectable levels at orchard establishment, at a rate consistent with its population doubling time. Relative abundance of *H. rhossiliensis* lagged behind the nematode, and the rate of increase in the incidence and prevalence of parasitism were slower than that of the nematode. In correlative analysis of predator and prey, we used the AUNDC to introduce a time component as a measure of the lag necessary to establish equilibrium after system disturbance. The nematode-density component of the AUNDC does not imply density-dependence in the predator-prey system because there is no mechanistic logic for the probability of attack by a predator being a function of the cumulative abundance of prey prior to the patch being invaded by the predator.

In the Livingston orchard, at least initially, *H. rhossiliensis* did not suppress population increase of the ring nematode. To increase the prevalence of parasitism, so that the prey is regulated at or suppressed to levels not damaging to trees, it is desirable to increase the slope of the relationship between prevalence of parasitism and AUNDC. The management challenge is to shorten the time requirement necessary for resurgence of the fungus after establishment of the orchard and to increase its predator-effectiveness. Augmentation might help, but alteration of the environment, to benefit the fungus and to enhance invasion of patches, is almost certainly necessary.

The common lines describing the relationships of both prevalence and incidence of parasitism with AUNDC suggest that there was no direct effect of rootstock on the process. Rootstocks influenced the para-

sitism parameters only through the indirect effect of the rate of increase of AUNDC. The difference in slopes of prevalence of parasitism on AUNDC as affected by phenamiphos suggests that the nematicide treatment may have a direct or indirect effect on the fungus as well as the nematode.

The effect of the high-level fall UAN-32 nitrogen application that suppressed *M. xenoplax* in all treatment combinations also reduced the prevalence of parasitism by *H. rhossiliensis* (data not shown). In each treatment, the prevalence of parasitism dropped to less than 1% of the surviving nematodes, although the effect was far less severe on incidence of parasitism by the fungus. However, the prevalence of parasitism recovered; 8 months after the UAN-32 application, it returned to the trajectory suggested by the regression analyses. Therefore, we infer that NH_3 , or some other derivative of UAN-32, may affect the fungus detrimentally when applied at high rates. The subsequent resurgence of the prevalence of parasitism may have been due to increased frequency of contact of the surviving nematode population with a flush of sporulating hyphae from nematode cadavers.

The nematode dosage model is useful for monitoring the probable impact of ring nematode on *Prunus* trees through time and for economic analysis of the effects of various treatments (rootstocks and nematicides). The impact of BC, including death of branches and trees, and its relationship to the Nemaguard rootstock and high population densities of the ring nematode, were economically more important than the direct impact of the nematode on crop yield. Observational evidence suggests a strong relationship between BC and the stunting of feeder roots during early years of tree growth (University of California Integrated Pest Management, 2002). Because the abundance of these roots is least, and their functional significance arguably greatest, in young, establishing trees, the predisposing damage may occur before differences in ring nematode dosage trajectory become detectable. In spring of the second year at the Escalon site, tree death and BC symptoms occurred in plots not treated with nematicide the previous fall. That is in concurrence with the general experience, based on observation but not experimental data, that while nematicide treatments earlier in the year may reduce ring nematode populations, fall nematicide treatment is necessary to reduce the incidence of BC the following spring (University of California Integrated Pest Management, 2002).

The mechanisms through which *M. xenoplax* and other stresses predispose *Prunus* trees to BC and PTSL remain uncertain; however, evidence is accumulating. For example, differences in rates of carbohydrate depletion and accumulation of the cyanide degradation product of prunasin, a cyanogenic glycoside, have been attributed to large numbers of *M. xenoplax*. Prunasin increased in roots and decreased in stem tissue in

the presence of the nematode, but it was unclear whether degradation of prunasin in stems was the result of tissue damage or its cause (Reilly et al., 1988). In a container experiment, *M. xenoplax* reduced plant dry weight and concentrations of starch and soluble carbohydrates in Nemaguard but not in tolerant BY520-9 rootstocks; however, prunasin content was not affected by *M. xenoplax* in either rootstock. Olien et al. (1995) speculated that carbohydrates in scions on Nemaguard rootstock are reduced by increased partitioning from shoots to roots and shifts in proportional composition of individual sugars. Consequently, tree injury occurs with environmental and biological stresses that do not injure healthy trees. Activity of polyphenol oxidase and peroxidase in trees with high numbers of *M. xenoplax*, and seriously affected by PTSL, was less than half those in healthy trees. That suggested that progressive weakening of the trees decreased their tolerance to PTSL; however, *M. xenoplax* was not implicated empirically as the cause of reduced enzyme activity (Gomes et al., 2000). While our studies do not add directly to understanding of the mechanisms, the hypothesis of cumulative nematode dosage as a stressor is consistent with the inferences regarding progressive weakening of trees.

A pest management conundrum was demonstrated in our studies. Nemaguard rootstock is used in *Prunus* orchards because it is resistant to root-knot nematode (*Meloidogyne* spp.). Lovell rootstock is susceptible to that nematode, although it may become more tolerant as an orchard matures. This is an example of a rootstock selected and used for resistance to one nematode species having greater susceptibility to another nematode species and, in certain conditions, being involved in an even more serious disease complex.

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