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Host Suitability and Response of Asparagus Cultivars to *Meloidogyne* Species and Races[1]

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Abstract: The host-parasite relationships of asparagus and *Meloidogyne* spp. were examined under greenhouse and microplot conditions. *Meloidogyne* species and races differed greatly in their ability to reproduce on asparagus seedlings. *Meloidogyne hapla* generally failed to reproduce, and *M. javanica, M. arenaria* race 1, and *M. incognita* race 3 reproduced poorly, with a reproduction factor (Rf = final population/initial population) usually < 1.0. Only *M. arenaria* race 2 and *M. incognita* races 1 and 4 reproduced consistently on all asparagus cultivars tested (Rf typically 1–11). No effect of *M. incognita* race 4 on host growth was detected. *Meloidogyne arenaria* race 2 and *M. incognita* race 1 had slight negative effects (5–10%) on plant and root growth.

Key words: asparagus, *Asparagus officinalis,* damage potential, *Meloidogyne* spp., nematode, population dynamics, resistance, root-knot nematode, tolerance.

The capacity of common species and races of *Meloidogyne* to reproduce on, and cause damage to, asparagus (*Asparagus officinalis* L.) has received only limited attention. Most studies to date provide an unclear picture of the status of asparagus as a host for root-knot nematodes. Evidence from several locations suggests that these nematodes can reproduce on asparagus. *Meloidogyne incognita* has been identified in asparagus plantings in Peru (5). Race 1 of the same species was recently isolated from established commercial asparagus stands in North Carolina (11).

Other reports indicate that asparagus may be resistant to *Meloidogyne* spp. Crittenden (4) described the common cultivar Mary Washington as being resistant to *M. incognita* var. *acrita* (= *M. incognita* (Kofoid & White) Chitwood) (10). The lack of galls on roots of asparagus grown in nematode-infested soil led to the conclusion that the plants were resistant (4). Cultivar Martha Washington has also been described (7) as resistant to root-knot nematodes, specifically *M. hapla* Chitwood. Further reports (3) of resistance have been based on the ability of asparagus to suppress *Meloidogyne* soil populations in the field (3, E. L. Nigh, Jr., pers. comm.). Greenhouse studies (12) with cultivar UC 500 and *M. incognita, M. arenaria* (Neal) Chitwood, *M. hapla,* and *M. javanica* (Treub) Chitwood led to the hypothesis that asparagus may become increasingly resistant to these nematodes as the plants age. A recent study (6) showed that populations of *M. incognita* developed more readily than those of *M. javanica* or *M. arenaria* on selected cultivars but had no effect on crown weight, and *Meloidogyne hapla* reproduced little on any cultivar.

Both the ability of the nematodes to reproduce on a host and the growth response of an infected host should be considered when describing a host as intolerant, tolerant, susceptible, or resistant to nematodes (15). Conflicting reports of suitability of asparagus for root-knot nematodes might thus be more clearly resolved. Our present studies were undertaken to clarify the host–parasite relationship of asparagus and *Meloidogyne* spp. In addition, the nematodes' effect on growth of asparagus, both in the greenhouse and in microplots, was examined. Such information is vital in determining the impact that *Meloidogyne* spp. might have on asparagus production in areas, such as the coastal plain of North Carolina, where these nematodes are virtually ubiquitous.

Materials and Methods

Nematode populations: All root-knot nematodes were propagated on tomato

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(*Lycopersicon esculentum* Mill. cv. Rutgers) in the greenhouse at 26–28 C. Populations used included *M. hapla, M. javanica,* and *M. incognita* race 3, all originally isolated from a tobacco rotation study in Rocky Mount, North Carolina. *Meloidogyne arenaria* race 1 from peanut (*Arachis hypogaea* L.), *M. arenaria* race 2 and *M. incognita* race 4 from resistant tobacco (*Nicotiana tabacum* L.), and *M. incognita* race 1 isolated from asparagus in Sampson County, North Carolina, were also used. Nematode populations had been previously identified by perineal pattern, male head morphology, and the North Carolina differential host test (8). Eggs for inoculations were extracted by the NaOCl method (9).

Plant material: In one experiment, asparagus crowns (Martha Washington Princeville) were obtained from a local source (G. D. Jackson, Joan of Arc Co., Turkey, NC) and held at 13 C until used. Seedlings were utilized in all other tests. Commercial cultivars included Pedigreed Washington (Wyatt-Quarles Seed Co., Raleigh, NC), Mary Washington (W. Atlee Burpee Co., Warminster, PA), and Viking and Viking KB3 (Stokes Seeds, Inc., Buffalo, NY). Seeds of asparagus hybrids were obtained from the Rutgers Research and Development Center, Bridgeton, NJ. Hybrids included Jersey Giant (56 × 22-8), Jersey General (362M × 22-8), Jersey King (Md 10 × 22-8), and Jersey Knight (277C × 22-8).

General experimental procedures: All greenhouse experiments were conducted with steam-sterilized clay pots (10 or 15 cm d). Asparagus seeds were germinated in Metro-mix potting medium (Grace Horticultural Products, Cambridge, MA). About 14 days after emergence, seedlings were transplanted, one per pot, into a steam-pasteurized 1:1 sand-soil mixture (85% sand, 10% silt, 5% clay).

Seedlings were inoculated by pouring NaOCl-extracted nematode eggs over the root system at transplanting. Roots were covered with soil, and pots were watered lightly. Uninfected controls were included in all tests. Plants were maintained in the greenhouse for ca. 60 days after inoculation. They were watered twice daily and fertilized weekly with Peter's 20-20-20 professional fertilizer (Peter's Fertilizer Products, Fogelsville, PA).

Unless indicated otherwise, ferns were cut at the soil line and weighed. Roots were separated from the soil by carefully shaking and rinsing them under running water; they were then dried with paper towels. The root portion was estimated as 88% of the total crown and root of the plant. In some tests, crown and root were weighed separately.

For nematode egg extraction, roots were cut into small pieces and mixed, and random 5-g subsamples were processed with the NaOCl method (1). Second-stage juveniles in a 500-cm^3 sample of the soil from each pot were extracted by elutriation and centrifugation (2). Both eggs and juveniles were counted, and total numbers per plant were calculated.

A randomized complete block design was used in all experiments. Unless indicated otherwise, nematode population data were subjected to a $\log_{10}(x + 1)$ transformation before statistical analyses.

Experiment 1: Seedlings of two asparagus cultivars, Mary Washington and Pedigreed Washington, were used to determine the reproductive ability of the seven described nematode populations and their impact on plant growth. Tests with each cultivar were repeated once. The first screening on Pedigreed Washington was carried out with ca. 20,000 nematode eggs per 15-cm-d pot; each treatment was replicated six times. The other tests were conducted utilizing 10-cm-d pots with ca. 10,000 eggs each. All treatments, including healthy controls, were replicated five times.

Reproduction factors (Rf = Pf/Pi) were calculated on a per plant basis using nontransformed nematode data. Statistical analyses were performed on plant data (shoot weight, root weight, and crown weight) and nematode reproduction factors (13). Analysis of variance was used to

determine treatment significance, and treatment means were separated by the Waller-Duncan k-ratio *t*-test.

Experiment 2: Initial evaluation of cultivars was performed in 15-cm-d pots with ca. 20,000 nematode eggs per pot, with separate testing for each nematode species and race. Populations of *M. arenaria* race 2 and *M. incognita* races 1 and 4 were selected for cultivar screening on the basis of preliminary testing. The final evaluation consisted of eight cultivar and four nematode treatments including a control, replicated five times. Plants in 10-cm-d pots were inoculated with ca. 10,000 nematode eggs. The experiment was harvested one block at a time beginning 60 days after inoculation.

Reproduction factors were calculated on a per plant basis using nontransformed nematode data. Statistical analyses, performed on nematode population data, nontransformed plant data, and Rf, included analysis of variance and the Waller-Duncan k-ratio *t*-test.

Experiment 3: A series of greenhouse experiments was performed to assess the effects of different population densities of *M. arenaria* race 2 and *M. incognita* races 1 and 4 on growth of Mary Washington asparagus in pot culture. All seedlings were grown in 15-cm-d clay pots.

Five initial population levels of each of the three nematode races were included in these studies: 0, 250, 5,000, 10,000, and 25,000 eggs per 500 cm^3 soil. Tests with *M. arenaria* race 2 and *M. incognita* races 1 and 4 were carried out twice. In a third test with *M. incognita* race 1, plants were not fertilized and were watered only once daily, resulting in poor growth. Eight replicates of each nematode level were used in the first study. Five replicates were used in subsequent studies.

Nematode population and plant growth data were subjected to regression analyses. Plots of residuals were used to determine the validity of using untransformed or $\log_{10}(x + 1)$ transformed initial population levels in the regressions.

Experiment 4: A study was conducted in microplots at the Central Crops Research Station, Clayton, North Carolina, to assess the effects of different population densities of *M. incognita* race 1 on asparagus growth and yield under field conditions. The microplots, which contained a Fuquay sand (91% sand, 6.5% silt, 2.5% clay; 0.6% OM, pH 6.1), were fumigated during the fall with 98% methyl bromide: 2% chloropicrin at the rate of 90 g/m^2 under polyethylene cover.

Inoculum for microplots consisted of chopped, infected roots and infested soil from the greenhouse cultures of *M. incognita* race 1. Randomly chosen subsamples were processed to determine nematode levels (2,3). Sufficient steam-pasteurized soil was added to the appropriate amount of inoculum to bring the volume to 5 liters per plot. Nematode treatment levels were 0, 100, 500, 2,500, 7,500, 15,000, 20,000, and 25,000 eggs and juveniles per 500 cm^3 soil, and tests were replicated four times. Chlamydospores (ca. 1,000) of the mycorrhizal fungus *Glomus macrocarpus* Tul. & Tul. were added to the root and soil mixture for each plot.

Plots were established on 18 March 1988. The nematode mixture was incorporated to an 18-cm depth in the center strip of each plot (ca. 18 cm wide × 76 cm long) after 110 g lime and 50 ml 12-6-24 fertilizer were added. Four Martha Washington Princeville asparagus crowns were then planted into the center strip. Additional nematode inoculum was added outside the center strip of each plot on 27 May 1988. Plots were watered as needed, and plants were sprayed with fungicide as needed during the summer to control *Cercospora* leafspot.

Nematode population densities were assessed on 1 July 1988, 11 October 1988, and 26 May 1989. Six 20-cm-deep soil cores were removed from around the crowns in each plot. Nematodes were extracted from a 250-cm^3 subsample by elutriation followed by centrifugation for juveniles (2), and eggs were extracted from

roots with NaOCl (1). On 15 November 1988, dead ferns were cut back to just above the soil line and weighed. Asparagus spears were harvested by hand from 30 March to 26 April 1989. Selection of spears for harvest was highly subjective, with height and thickness being the main criteria. Total weight of spears and stand count were recorded. Regression analysis was used in an effort to relate plant growth data to nematode population densities.

The infested asparagus stands in microplots were sampled to assess downward migration of *M. incognita* race 1 in the soil and along the asparagus roots. Twelve different plots were sampled on each of two sampling dates: 26 May and 22 June 1989. Only plots that had been infested the previous spring and had showed good stand growth were selected for sampling. Two points close to the asparagus crowns were sampled at four depths: 0–15 cm, 15–30 cm, 30–45 cm, and 45–60 cm. An 8-cm-d bucket auger was used to collect all samples except those at the lowest depth in the first sampling. The abundance of clay at that level necessitated the use of a 5-cm-d auger. Soil from the two sampling points for a given depth in each plot was mixed, and a 500-cm^3 subsample was processed. Roots and soil were separated by elutriation (2). Juveniles were extracted from soil by centrifugation. Roots were weighed prior to egg extraction by the NaOCl method (1). Roots from the first sampling were weighed without being thoroughly cleaned; roots in the second set were carefully separated from soil and other debris before being weighed.

Results

Experiment 1: None of the nematode races significantly affected either shoot, root, or crown weight of Pedigreed Washington and Mary Washington asparagus, although slight differences existed (Table 1). In the first trial on Pedigreed Washington, control plants, *M. arenaria* race 1, and *M. incognita* race 1 treatments showed bet-

TABLE 1. Growth of two asparagus cultivars in soil infested with selected *Meloidogyne* species and races and related nematode reproduction after ca. 60 cays in pot culture in the greenhouse (experiment 1).

Treatment	Fresh weight: Shoot Test A	Fresh weight: Shoot Test B	Fresh weight: Plant Test A	Fresh weight: Plant Test B	Reproduction factor (R_f) Test A	Reproduction factor (R_f) Test B
			Pedigreed Washington			
Control	29.1 ab	18.4 a	64.8 a	73.6 a		
M. hapla	31.9 ab	20.9 a	60.8 ab	65.3 a	0.0 c	<0.1 b
M. javanica	28.6 ab	17.0 a	56.8 ab	48.7 a	<0.1 c	0.2 b
M. arenaria race 1	38.3 a	17.5 a	72.4 a	61.1 a	<0.1 c	<0.1 b
M. arenaria race 2	22.4 b	15.4 a	39.0 b	52.0 a	0.3 c	0.9 b
M. incognita race 1	33.6 ab	21.0 a	65.3 a	77.3 a	0.7 b	5.8 a
M. incognita race 3	26.9 ab	16.7 a	49.4 ab	64.5 a	0.1 c	0.2 b
M. incognita race 4	30.6 ab	19.6 a	56.5 ab	66.4 a	2.0 a	5.6 a
			Mary Washington			
Control	17.9 a	15.5 a	63.1 a	66.0 a		
M. hapla	14.8 a	15.7 a	40.7 a	62.9 a	0.0 b	0.1 c
M. javanica	14.8 a	17.3 a	56.4 a	76.8 a	0.4 b	3.1 bc
M. arenaria race 1	17.1 a	17.5 a	65.4 a	77.2 a	0.3 b	0.4 c
M. arenaria race 2	15.9 a	16.7 a	64.2 a	60.5 a	1.8 b	3.1 bc
M. incognita race 1	15.1 a	13.6 a	49.5 a	52.2 a	9.2 a	7.0 ab
M. incognita race 3	17.7 a	16.0 a	61.3 a	62.8 a	0.6 b	0.5 c
M. incognita race 4	15.3 a	15.6 a	52.5 a	62.7 a	2.7 b	11.1 a

Values are means of five replicates. The initial inoculum (Pi) was 10,000 eggs/10-cm-d pot except test A Pedigreed Washington, which had 20,000 eggs/15-cm-d pot.

Means followed by the same letter within a column are not different ($P < 0.05$) according to the Waller-Duncan k-ratio *t*-test (k-ratio = 100).

ter growth than plants grown in soil infested with *M. arenaria* race 2. When compared to the healthy control treatment, overall growth of Mary Washington seedlings was unaffected by any nematode. Nematodes that reproduced on Pedigreed Washington and Mary Washington induced only small, discrete root galls and egg masses; otherwise, the root systems were extensive and healthy in appearance, with abundant feeder roots.

Major differences in reproduction existed among nematode populations ($P < 0.01$). On Pedigreed Washington, *M. incognita* races 1 and 4 reproduced better than the other nematodes. Reproduction of all nematodes, as measured by total numbers of eggs and juveniles and Rf values, was greater in the second run of the test (Table 1). *Meloidogyne hapla* did not reproduce on either cultivar. Patterns of reproduction for the other nematodes were slightly different on the two cultivars. Races 1 and 4 of *M. incognita* and *M. arenaria* race 2 reproduced well on Mary Washington in both tests. *Meloidogyne javanica* reproduced well in the second trial on Mary Washington but did poorly on Pedigreed Washington in both tests. Race 1 of *M. arenaria* and *M. incognita* race 3 did not increase, with Rf < 1.0.

Experiment 2: Initial screening indicated that *M. arenaria* race 2 and both races 1 and 4 of *M. incognita* were able to parasitize all asparagus cultivars to some extent (data not shown). Reproduction of *M. arenaria* race 2 was not as great as that of *M. incognita* races 1 and 4.

In the final factorial experiment, root and overall plant growth were affected by nematode treatment (Table 2). Race 2 of *M. arenaria* suppressed ($P < 0.05$) root and shoot growth. Cultivar also affected root and total plant weight ($P < 0.01$). Block had a highly significant effect on all plant parameters ($P < 0.05$), as well as on nematode reproduction factors ($P < 0.05$). No significant interaction of treatment and cultivar was detected.

Reproduction differed among *Meloidogyne* races. Races 1 and 4 of *M. incognita* had an Rf of 4 to 5, compared to an Rf of 1.1 for *M. arenaria* race 2. All cultivars tested were suitable hosts for the three nematodes, although some allowed slightly less reproduction than others. Mean Rf for the three nematode races per cultivar were similar: Viking = 3.1, Viking KB3 = 4.4, Jersey Giant = 4.8, Jersey General = 3.5, Jersey King = 5.5, Jersey Knight = 2.2, Mary Washington = 2.3, and Pedigreed Washington = 2.7.

Experiment 3: Regressions of plant growth data on Pi indicated that *M. incognita* race 4 had no impact on growth of Mary Washington asparagus seedlings in greenhouse cultures. Race 2 of *M. arenaria* slightly suppressed shoot growth in one experiment, but the coefficient of determination (R^2) was low (0.12). Race 1 of *M. incognita* (asparagus isolate) suppressed 'plant' and root growth in two out of three

TABLE 2. Composite host response and relative reproduction of *Meloidogyne arenaria* race 2, *M. incognita* race 1, and *M. incognita* race 4 on eight asparagus cultivars in the greenhouse (Experiment 2).

Parameter	Control (no nematodes)	*M. arenaria* race 2	*M. incognita* race 1	*M. incognita* race 4
Plant growth fresh weight (g):				
Shoot	21.7 a	20.4 a	21.0 a	21.3 a
Root	46.0 a	39.5 b	40.8 ab	41.6 ab
Plant	67.7 a	59.9 b	61.8 ab	62.9 ab
Nematode reproduction:				
Total eggs + J2 (per plant)		11,362 b	47,669 a	43,518 a
Reproduction factor (Pf/Pi)		1.1 b	4.8 a	4.4 a

Values are means of 40 replicates and eight asparagus cultivars: Viking, Viking KB3, Jersey Giant, Jersey General, Jersey King, Jersey Knight, Mary Washington, and Pedigreed Washington. Initial inoculum was 10,000 eggs/pot.

Means followed by the same letter within a row are not different ($P < 0.05$) according to the Waller-Duncan k-ratio *t*-test (k-ratio = 100); $\log_{10}(x + 1)$ transformation used for nematode numbers.

experiments but had no effect on shoot growth. Coefficients of determination were also very low (0.22–0.26) for the significant ($P < 0.01$) regression equations (most models not included).

Regressions of Pf on Pi were significant for all tests except the first one with *M. arenaria* race 2. Levels of significance for the regression models were much greater for *M. incognita* races 1 and 4 than for *M. arenaria* race 2. The R^2 values tended to be fairly low (0.20–0.63) for all the nematodes, indicating that nematode reproduction was dependent on other factors besides the number of nematodes added to a pot. Nematode reproduction was greatest by far in the third test with *M. incognita* race 1, when plants were subjected to decreased water and nutrient levels. The regression equation for that trial was $Pf = 11{,}786 + 12.8\,Pi - 4.82 \times 10^{-4}\,Pi^2$ ($R^2 = 0.62$). Although only a small portion of the total root system was parasitized by nematodes in other tests, the entire root system of each nematode-treated plant was parasitized in that experiment.

Experiment 4: Meloidogyne incognita race 1 became well established in the microplots, with soil populations reaching near 50,000/500 cm^3 soil (Table 3). With the lowest Pi, 100 eggs/500 cm^3 of soil, the Rf for the first 7 months was >300 compared to 1.6 for a Pi of 25,000. Carryover populations from fall to spring were low (Tables 3,4) but increased by early summer. Eggs, juveniles, and host roots were detected at all soil depths (up to 45–60 cm) sampled in both May and June, 1989. No effects of nematode population densities on asparagus growth were found (data not shown). Coefficients of determination for regression equations relating fern growth and yield of asparagus spears to Pi or to nematode population densities in July, October, and May were extremely low (<0.10). In addition, none of the regression models were significant. The low initial nematode infections of the control plants used in this test were not maintained at detectable levels.

TABLE 3. Soil populations of *Meloidogyne incognita* race 1 developing on asparagus cv. Martha Washington Princeville in microplots at the Central Crops Research Station, Clayton, North Carolina (experiment 4).

	Eggs and J2 per 500 cm^3 soil		
Pi†	1 July 1988	10 Nov 1988	26 May 1989
0	577	10	0
100	2,225	30,909	601
500	2,450	39,891	1,227
2,500	1,689	33,966	527
7,500	8,249	42,599	721
15,000	2,756	34,362	468
20,000	6,113	48,286	1,179
25,000	8,920	40,873	513

Six soil cores taken from each plot were combined; a 250-cm^3 sample was used for nematode extraction. Values are means of four replicates.

† Pi was based on the volume of infested soil and roots incorporated into each microplot on 18 March 1988. The early detections in the 0 control came from the use of *Meloidogyne*-infected crowns.

DISCUSSION

Asparagus roots contain the toxic compound asparagusic acid (14), which is nematicidal in solution under laboratory conditions (16). No definitive evidence indicates that this compound protects asparagus roots fully from nematodes under

TABLE 4. Relative root growth of asparagus cultivar Martha Washington Princeville, planted 18 March 1988, and populations of *Meloidogyne incognita* race 1 at different soil depths in microplots, Central Crops Research Station, Clayton, North Carolina (experiment 4).

Soil depth (cm)	Roots (g)	Eggs 500 cm^3 soil	J2 500 cm^3 soil	Eggs/g root
		26 May 1989		
0–15	17.5 a	529 a	167 b	29 a
15–30	16.2 a	330 a	550 ab	24 a
30–45	7.6 b	1119 a	690 a	170 a
45–60	0.7 c	23 b	68 c	12 b
		22 June 1989		
0–15	13.7 a	3672 a	275 bc	265 a
15–30	12.9 a	2031 a	698 a	187 a
30–45	5.8 b	1250 b	516 ab	173 a
45–60	2.9 c	291 b	304 c	140 a

Means followed by the same letter within a column are not different ($P < 0.05$) according to the Waller-Duncan k-ratio *t*-test (k-ratio = 100). Nematode data, including eggs/g root, were $\log_{10}(x + 1)$ transformed before analysis.

Each value is the mean of 12 samples. Different plots were sampled each date.

normal growing conditions. Asparagusic acid is a simple compound (15) that probably is degraded quickly by soil microbes. Young seedlings and small roots clearly supported more nematode reproduction than older roots of established plants. Similar findings were recorded in another study (6).

Our studies indicate that most asparagus cultivars may serve as good hosts for several root-knot nematodes, including *M. arenaria* race 2 and *M. incognita* races 1 and 4. However, asparagus was not a good host for all the nematodes tested. *Meloidogyne hapla* did not reproduce on any of the cultivars tested. Esmenjaud *et al.* (6) obtained almost identical results with other cultivars. On the basis of nematode reproduction alone, asparagus may be described as highly resistant to *M. hapla, M. javanica, M. arenaria* race 1, and *M. incognita* race 3.

The similarity among asparagus cultivars in their host suitability for reproduction of *M. arenaria* race 2, *M. incognita* race 1, and *M. incognita* race 4 probably reflects the lack of genetic variability in cultivated asparagus in the United States. This uniformity could pose difficulties in maintaining high levels of resistance to these nematodes. However, the relatively low populations of these nematodes recovered from asparagus in our studies, as compared to the high populations occurring on susceptible tomato, indicate that a certain level of resistance to these nematodes probably is functional in all asparagus cultivars.

The lack of obvious damage to asparagus root systems infected with root-knot nematodes indicates that these parasites generally have little impact on host growth. This assumption is supported by our greenhouse and microplot studies. Although some relationships between nematode population density and host growth were found for *M. arenaria* race 2 and *M. incognita* race 1, the effects of nematodes were minor. However, plants grown under nutrient-moisture stress were more sensitive to *M. incognita,* and this could have implications for plants in the field. On the basis of both nematode and plant-growth data from these studies, and other recent research (6), asparagus may be further described as resistant to most *Meloidogyne* races. Because *M. incognita* races 1 and 4 were able to reproduce well but had little impact on asparagus growth, the host could be described as tolerant to these particular nematodes. In contrast, this crop is essentially a nonhost for *M. hapla.*

The low population densities of naturally occurring populations of *Meloidogyne* in established fields (11) and the lack of reported damage by root-knot nematodes in commercial asparagus plantings support the conclusions presented here and by Esmenjaud et al. (6). Still, insidious infections of "transplant" crowns and field infestations may interfere with effective management of these nematodes on susceptible crops. Although the low levels of contaminating nematodes failed to increase as rapidly as the plants grew, they also could have long-term negative effects on asparagus stands.

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