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Seasonal Migration of *Meloidogyne chitwoodi* and its Role in Potato Production[1]

H. MOJTAHEDI,[2] R. E. INGHAM,[3] G. S. SANTO,[2]
J. N. PINKERTON,[2] G. L. REED,[4] AND J. H. WILSON[2]

Abstract: Seasonal vertical migration of *Meloidogyne chitwoodi* through soil and its impact on potato production in Washington and Oregon was studied. Nematode eggs and second-stage juveniles (J2) were placed at various depths (0–180 cm) in tubes filled with soil and buried vertically or in holes dug in potato fields. Tubes were removed at intervals over a 12-month period and soil was bioassayed on tomato roots. Upward migration began in the spring after water had percolated through the tubes. Nematodes were detected in the top 5 cm of tubes within 1–2 months of burial, depending on depth of placement. Potatoes were grown in field plots for 4 or 5 months before the tubers were evaluated for infection. One hundred eggs and J2 per gram soil placed at 60 and 90 cm caused significant tuber damage at the Washington and Oregon sites, respectively. At the Washington site, inoculum placed at 90, 120, and 150 cm caused potato root infection without serious impact on tuber quality, but inoculum diluted 2–8 times and placed at 90 cm did not cause root or tuber infection. Nematode migration was dependent on soil texture; 9 days after placement at the bottoms of tubes, J2 had moved up 55 cm in sandy loam soil (Oregon) but only 15 cm in silt loam (Washington). Thus, the importance of *M. chitwoodi* which occur deep in a soil profile may depend on soil texture, population density, and length of the growing season.

Key words: Columbia root-knot nematode, ecology, *Meloidogyne chitwoodi*, potato, recolonization, *Solanum tuberosum*, survival, vertical migration.

Meloidogyne chitwoodi Golden et al. is a major pest of potato (*Solanum tuberosum* L.) in the western United States (16). This nematode reduces tuber quality with preplant populations as low as 1 egg/250 cm^3 soil (17). Active *M. chitwoodi* second-stage juveniles (J2) have been recovered from soil collected as deep as 1.5 m (15). In the laboratory, ca. 1% of the *M. chitwoodi* J2 introduced to the bottoms of soil tubes migrated 50 cm upward to infect tomato roots within 9 days (13). Motile root-knot nematodes deep in soil can complicate management decisions. They are not detected by sampling only the upper 30–60 cm, as is commonly practiced in the Pacific Northwest; they are protected from environmental extremes; they escape physical (6) and chemical control practices (6,10); and they may move into treated soil, like stubby root nematodes (19), to render control measures ineffective. Nematodes may also migrate downward to escape adverse environmental conditions near the soil surface.

Long-distance vertical migration of other plant-parasitic nematodes in columns of soil within tubes under controlled and field conditions are documented (2,6,8,14). However, the impact of migrating nematodes to a field-grown crop has seldom been examined (7,8).

Our objectives were to study the vertical movement of *M. chitwoodi* in soil tubes during the year, and to evaluate the economic importance of nematodes deep in the soil to field-grown potatoes. A summary of these studies was reported previously (11).

MATERIALS AND METHODS

Seasonal migration in soil tubes: Tubes to hold soil columns were constructed from a series of rings (5 cm long × 8.25 cm d) cut from polyvinylchloride (PVC) pipe (13). A sandy loam soil (80.2% sand, 16.2% silt, 3.6% clay) was collected from a potato field where *M. chitwoodi* was known to occur as deep as 90 cm (12). A portion of the soil was fumigated with methyl bromide and

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[1] PPNS Paper No. 0068. Project No. 0240. College of Agriculture and Home Economics Research Center, Washington State University, Pullman, WA 99164.

[2] Research Associate, Professor, former Research Associate and Agricultural Technologist, Department of Plant Pathology, Washington State University, Irrigated Agriculture Research and Extension Center, Prosser, WA 99350.

[3] Assistant Professor of Nematology, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97330.

[4] Associate Professor of Entomology and Superintendent of Hermiston Agricultural Research and Extension Center, P.O. Box 105, Hermiston, OR 97838.

packed into tubes to obtain a bulk density of 1.34 g/cm^3. Water was percolated through the soil and then allowed to drain freely for 1 week. After drainage, the soil moisture was ca. 13% by weight.

To inoculate the first set of tubes, the untreated portion of field soil containing infective J2 plus eggs (9–10/g) was used. To inoculate the other tubes, fumigated soil was mixed with enough infected tomato root pieces to attain J2 plus egg density equal to field population, as determined by a tomato bioassay. The procedure included growing a 3-week-old tomato (*Lycopersicon esculentum* Mill. cv. Columbian) transplant in the soil for 3 weeks, then removing roots, staining them with acid fuchsin (1), and counting nematodes in roots. An inoculum chamber, constructed from two or three PVC rings, was packed with infested soil (ca. 430 g/ring) and fastened to the top or bottom of each tube. Two empty rings were then taped on top to avoid contamination from surrounding soil after burial. Tubes were placed vertically in a trench with the two empty rings above the soil surface, and buried at the Washington State University Irrigated Agriculture Research and Extension Center at Prosser. When tubes were excavated, the soil from each ring was bioassayed as described.

To study migration during the fall, winter, and early spring, eight 60-cm tubes with inoculum chambers on top and eight 60-cm tubes with bottom chambers were planted on 10 October 1985. Four tubes of each set were excavated and bioassayed on 19 November 1985 and 10 April 1986 (40 and 150 days after burial). To study migration during the spring and summer, four top-inoculated and four bottom-inoculated 60-cm tubes were buried on 15 May 1986 and excavated for bioassay on 25 August 1986 (100 days after burial). Tubes during the winter study received 100 ml water at the time of burial but none thereafter. Tubes in the summer study received 400 ml water every third day of the experiment. The soil temperature was recorded at 20 cm below the soil surface with a Datapod (Omnidata International, Logan, UT) recorder throughout the experiment.

To study upward migration toward a host, a plant chamber for confining root growth was constructed by joining two PVC rings and sealing the bottom with 28-μm-mesh nylon fabric. The chamber was then filled with fumigated soil, into which was transplanted a 3-week-old tomato seedling. Four tubes of 60-cm, 120-cm, or 180-cm length with inoculum chambers on bottom and plant chambers on top were buried on 28 April 1987. Tubes received 400 ml water every 3 days. The plant chambers were removed and replaced with new ones monthly for 4 months. The migration of infective *M. chitwoodi* was monitored by counting the number of nematodes that had penetrated the tomato roots. The 180-cm tubes were removed and bioassayed after 5 months; the 60-cm and 120-cm tubes were bioassayed after 12 months.

Upward movement of M. chitwoodi J2 in potato field: Farm sites were selected at Prosser, Washington, and Hermiston, Oregon. At Prosser, soil texture changed with depth and was classified as sandy loam (49–52% sand, 43–47% silt, 2–4% clay) from 0 to 60 cm and as silt loam (41–43% sand, 52–55% silt, 2–4% clay) from 90 to 150 cm. At Hermiston, soil texture was uniform throughout the 120-cm profile and classified as loamy sand (76–78% sand, 16–17% silt, 5–7% clay). The Prosser site was fumigated with 1,3-dichloropropene (273 liters/ha) 1 month before planting. The Hermiston site was without previous root-knot nematode infestation history. Nonetheless, both sites were sampled at different depths to ascertain the absence of root-knot nematode species before planting.

In the spring of 1988 and 1989, potato seed pieces (certified Russet Burbank) were planted 15 cm deep, 22.5 cm apart in 85-cm-spaced rows. After planting, seed pieces were removed at 135-cm (Prosser) or 240-cm (Hermiston) intervals along every other row, and 30-cm-d holes were augered to depths of 30, 60, 90, and 120 cm (or 150 cm at Prosser) unless indicated oth-

erwise. One hole was dug to each depth in each of five rows in a randomized complete block design. Five hundred grams of soil infested with eggs + J2 of *M. chitwoodi* (100/g) was funneled to the bottom of each hole through a PVC pipe. The excavated soil was returned to the holes and tamped to restore soil continuity, and seed pieces were replanted. The potato hills under which nematodes were buried were referred to as target hills. As a separate control treatment, inoculum was placed in direct contact with seed pieces and covered with soil. After plant emergence, the plots were irrigated by sprinklers as needed and otherwise maintained according to standard commercial practices (9).

Four (Prosser) and five (Hermiston) months after planting, the tubers from target and adjacent hills in the same row were collected and rated for nematode infection on a scale of 0–6 where 0 = 0 infection site, 1 = 1–10, 2 = 11–25, 3 = 26–50, 4 = 51–75, 5 = 76–100, and 6 = more than 200 infection sites per tuber. An infection index was also assigned to each hill based on Σ (number of infected tubers per infection class × infection rating)/total number of tubers per hill. At the Prosser site, the potato vines were still green at harvest; therefore, root samples were collected and nematode eggs were extracted by shaking the roots in 1% sodium hypochlorite (4). The numbers of J2 per 250 cm^3 soil collected from around the potato tubers were also determined after centrifugal-flotation extraction (5). At the Hermiston site, soil samples were taken from soil directly around tubers (0 depth) and at 30 cm increments to 120 cm; J2 were extracted by Baermann funnels.

In the 1988 study at Prosser, one inoculum density—100 eggs and J2/g—was placed at different depths, whereas in 1989, five different inoculum densities—0, 12, 25, 50, or 100 eggs and J2/g (produced by diluting the original inoculum with clean soil)—were placed at a single depth of 90 cm to determine the damage threshold level of deep-occurring *M. chitwoodi* on Russet Burbank potato. At Hermiston, the infested soil inoculum contained 100 and 10 infective eggs and J2/g for the 1988 and 1989 trials, respectively.

Soil type study: To compare the suitability of Prosser and Hermiston soils for nematode movement, eight 60-cm tubes were constructed, and four were filled with Prosser and four with Hermiston soil to obtain bulk densities of 1.26 and 1.49 g/cm^3 of soil, respectively. The tubes were watered to field capacity, and 5,000 freshly hatched (18) *M. chitwoodi* J2 were injected through a port in the bottom ring. The columns were incubated at 15–18 C for 9 days before they were disassembled and each ring was bioassayed with a tomato seedling.

The data were analyzed by ANOVA and treatment means were separated by Duncan's multiple-range test.

Results

Seasonal migration study: Less than 1% of the nematode population migrated out of the inoculum chambers in either direction. However, there was a distinct seasonal pattern of migration (Tables 1, 2). During late fall (10 October–19 November), the nematodes moved only 5–10 cm in either direction from the inoculated depth. Bioassay tests indicated that 9 and 12% of the original inoculum survived 40 days in the top and bottom inoculum chambers, respectively. During this period there was only 8 mm precipitation and the mean ambient air temperature dropped from 10 C in October to −5 C in November (283 to 333 Julian days). Similarly, mean soil temperature at 20 cm below the soil surface dropped gradually from 10 to 2 C (Fig. 1).

From 10 October to 10 April (292 to 110 Julian days), the vertical distribution of *M. chitwoodi* remained virtually unchanged, with only a few nematodes migrating 20 cm above the inoculum chamber in one replicate (Table 1). Downward migration occurred in all replicates, however, and nematodes were detected as deep as 30 cm below the last ring of the inoculum chambers (45 cm below the soil surface) (Table 2). Numbers of infective

TABLE 1. Upward migration of *Meloidogyne chitwoodi* in soil tubes buried in the field and excavated after 40, 150, and 100 days.

Distance from inoculum (cm)	Mean ± SE		
	40 (10 Oct–19 Nov)	150 (10 Oct–10 Apr)	100 (15 May–25 Aug)
+60	0 ± 0	0 ± 0	0 ± 0
+50	0 ± 0	0 ± 0	6 ± 2
+40	0 ± 0	0 ± 0	3 ± 0.4
+30	0 ± 0	0 ± 0	5 ± 1
+20	0 ± 0	3 ± 0.3	4 ± 1
+10	29 ± 27	16 ± 11	24 ± 12
0†	425 ± 72	169 ± 61	65 ± 20
0†	675 ± 99	138 ± 51	279 ± 68
0†	427 ± 78	255 ± 83	254 ± 40

Values are means of four replicates and represent the number of *M. chitwoodi* detected in tomato roots after a bioassay period of 3 weeks.

† Three-ring inoculum chamber at the bottom of each 60-cm tube, with 4,267 or 3,750 eggs and J2/ring in tubes buried 10 Oct or 15 May, respectively.

TABLE 2. Downward migration of *Meloidogyne chitwoodi* in soil tubes buried in the field and excavated after 40, 150, and 100 days.

Distance from inoculum (cm)	Mean ± SE		
	40 (10 Oct–19 Nov)	150 (10 Oct–10 Apr)	100 (15 May–25 Aug)
0†	318 ± 62	8 ± 6	0 ± 0
0†	500 ± 96	59 ± 32	0 ± 0
0†	350 ± 99	144 ± 58	5 ± 3
10	59 ± 18	32 ± 10	6 ± 2
20	0 ± 0	8 ± 4	0 ± 0
30	0 ± 0	2 ± 0.5	0 ± 0
40	0 ± 0	0 ± 0	0 ± 0
60	0 ± 0	0 ± 0	0 ± 0

Values are means of four replicates and represent the number of *M. chitwoodi* detected in tomato roots after a bioassay period of 3 weeks.

† Three-ring inoculum chamber assembled at the top of each 60-cm tube, containing 4,267 or 3,750 eggs and J2/ring in tubes buried on 10 Oct or 15 May, respectively.

nematodes in the inoculum chambers declined further to 1.7% and 4.5% of the original population in the top and bottom chambers, respectively. Precipitation during this period was 10 cm, and soil temperature at 20 cm ascended gradually from 0.4 C to 12 C. Soil in the top 20 cm was subjected to freezing frequently during the winter (Fig. 1).

From 15 May to 25 August (135 to 235 Julian days), the nematode inocula placed on the top of the tubes disappeared from the first and second ring, and only a few viable nematodes were present in the third ring of the inoculum chambers (Table 2). Nonetheless, a few nematodes migrated 10 cm downward (25 cm below the soil surface). During this 100-day incubation period, the tubes received 250 cm irrigation water and 3.5 cm rain. The mean soil temperature at 20 cm rose from 16 to 24 C and ambient temperature rose from 15 to 24 C. In contrast to the limited downward migration, the upward migration of *M. chitwoodi* was extensive during May through August (Table 1). Live nematodes were detected at 50 cm above the inoculum chambers, near the soil surface. During this period the number of viable nematodes in the bottom chambers declined to 4.5% of the original level.

In tubes with plant chambers, the time for *M. chitwoodi* to infect tomato roots near the surface depended on the depth of nematode placement. A small fraction of the nematodes moved upward 60 cm in 1 month and 120 and 180 cm in 2 months (Table 3). After 3 and 4 months, no additional nematodes were detected in the tomato roots. After 5 and 12 months, the numbers of infective nematodes in the inoculum chambers had declined to a small fraction of the original population.

Upward movement in potato fields: In the 1988 test at Prosser, *M. chitwoodi* migrated from all depths to infect potato roots (Table 4). In all cases, J2 were found in the soil around roots and (or) eggs were recovered from the root systems. However, greatest infection and damage to potato tubers was caused by those nematodes that were placed at 0, 30, and 60 cm below the seed piece. Nematodes from greater depths were rarely found within the tubers. Horizontal migration of *M. chitwoodi* was limited at the Prosser site; however, nematodes placed at 0 and 30 cm were able to migrate horizontally and cause damage to tubers on either side of the target plants. No tuber infection was observed in adjacent potatoes planted in the buffer rows. Potato tubers were formed at 15–20 cm

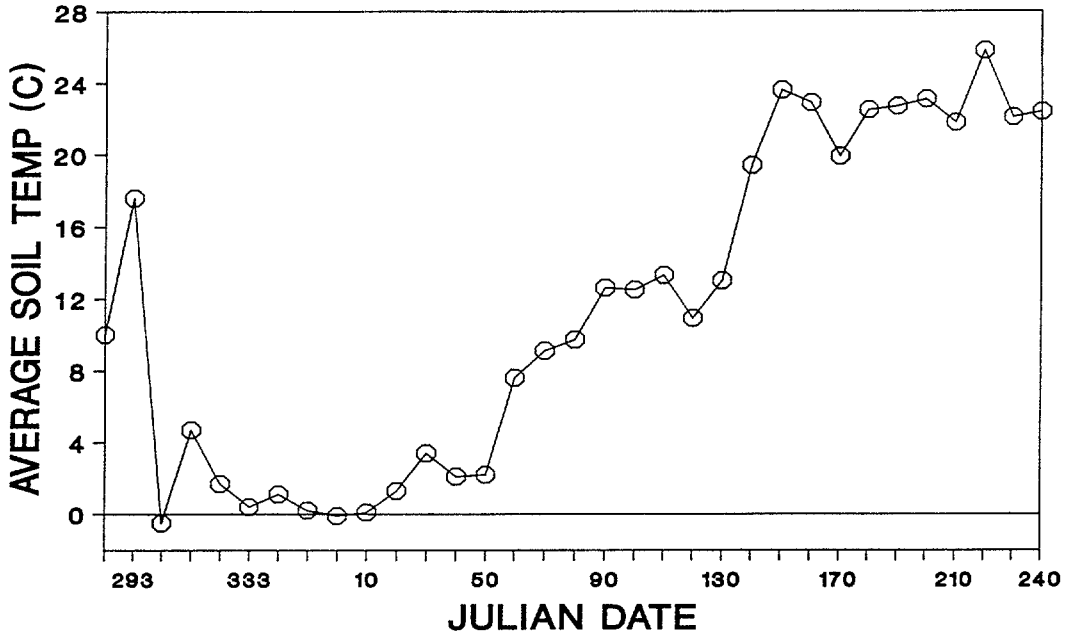

FIG. 1. Soil temperature (C) at 20 cm below the soil surface at Prosser, Washington, during October 1986 through August 1987.

below the soil surface and roots were found as deep as 45 cm.

In the 1989 inoculum density experiment at Prosser, only a few J2 from the highest inoculum density (100 eggs + J2) reached the rhizosphere from 90 cm. No tuber infection was observed on any plant (Table 5). Nematode distribution throughout the soil profile was not examined in this study.

The data for both years of the study at Hermiston were similar, and only those of 1988 are presented (Tables 6, 7). *Meloidogyne chitwoodi* migrated from all depths and infected tubers at target hills in both years. The intensity of damage (percentage of culls) was inversely correlated to the depth of placement of nematodes ($r = -0.99$) ($Y = 86.6 - 0.703X$). In 1988, tubers from hills adjacent to target hills were also infected by nematodes placed at all depths, although those from 120 cm did not cause serious damage on these tubers (Table 6). Furthermore, some tubers located 45 cm (two hills) from control hills (0-cm depth) were slightly (3% culls) damaged by *M. chitwoodi*. In 1989 some tubers from adjacent rows were also lightly in-

TABLE 3. *Meloidogyne chitwoodi* detected after 1–4 months in tomato roots planted on top of soil tubes buried in the field, and nematodes recovered in inoculum chambers at the bottom of soil tubes after 5 and 12 months.

Tube height (cm)†	Plant chamber (Mean ± SE)				Inoculum chamber (Mean ± SE)	
	1	2	3	4	5	12
60	10 ± 4	7 ± 4	0 ± 0	0 ± 0	—‡	1 ± 1
120	0 ± 0	3 ± 1	0 ± 0	0 ± 0	—	29 ± 20
180	0 ± 0	13 ± 12	0 ± 0	0 ± 0	1,521 ± 419	—

Values are means of four replicates and represent the number of *M. chitwoodi* detected in tomato roots after a bioassay period of 3 weeks.

† Inoculum chambers containing infested soil were attached to the bottom of each tube before burial on 28 April 1987.

‡ Not determined.

TABLE 4. *Meloidogyne chitwoodi* second-stage juveniles (J2) in soil, eggs recovered from root systems, infection index, and culls of potato tubers from plots with nematodes placed at different depths, Prosser, Washington.

Placement depth (cm)†	J2/250 cm³ soil (no.)	Eggs (no.)	Infection index‡	Culls (%)§
0	26,551 a	7,447 a	5.2 a	100 a
30	517 b	272 b	3.9 b	93 a
60	7 c	47 b	1.1 c	38 b
90	0 c	3 c	0.0 d	0 c
120	0 c	7 c	0.0 d	0 c
150	2 c	2 c	0.2 d	0 c

Values are means of five replicates. Means within a column followed by the same letter do not differ at $P = 0.05$ according to Duncan's multiple-range test.

† Soil (500 g) containing 100 eggs and J2/g was placed at the selected depth in each hole on 25 May, and potatoes were harvested on 3 October 1988.

‡ Infection index: number of infected tubers per infection class × infection rating ÷ total number of tubers per hill; based on infection rating where 0 = 0 sites, 1 = 1–10, 2 = 11–25, 3 = 26–50, 4 = 51–75, 5 = 76–100, and 6 = 200+ infection sites per tuber.

§ Tubers with six or more infection sites were graded as culls.

fected, indicating lateral migration had occurred across the row. Sampling of the soil profiles showed that, except for the 120-cm depth, nematodes migrated downward as well as upward. Nematodes placed at 120 cm may have migrated downward as well but were not sampled (Table 7).

Soil type study: Meloidogyne chitwoodi J2 migrated to the top of the columns (60 cm) in the Hermiston soil within 9 days. In contrast, J2 migrated only 15 cm upward in the Prosser soil during the same period (Table 8). In either case, only a fraction of the total nematodes introduced was detected by bioassay in soil above the point of nematode placement.

TABLE 5. *Meloidogyne chitwoodi* second-stage juveniles (J2) collected from around tubers, and root and tuber infection of potato from plots with different numbers of nematodes placed at the same depth, Prosser, Washington.

Nematodes placed† (no.)	J2/250 cm³ soil (Mean ± SE)	Root infection	Tuber infection
100	10 ± 2	+	−
50	0 ± 0	−	−
25	0 ± 0	−	−
12	0 ± 0	−	−
0	0 ± 0	−	−

Values are means of five replicates.

† Soil (500 g) containing specified eggs and J2/g was placed 90 cm deep in each hole on 15 May, and potatoes were harvested on 3 October 1989.

TABLE 6. Infection index and culls of potato tubers from target and adjacent hills in plots with *Meloidogyne chitwoodi* placed at different depths, Hermiston, Oregon.

Placement depth (cm)†	Target hills		Adjacent hills	
	Infection index‡	Culls§ (%)	Infection index‡	Culls§ (%)
0	4.2 a	87 a	1.8 a	39 a
30	2.4 b	62 ab	1.9 a	44 a
60	1.8 b	52 b	0.9 ab	31 a
90	0.4 c	17 c	0.3 b	6 b
120	0.4 c	4 c	0.1 b	0 b

Values are means of five replicates. Means followed by the same letter do not differ at $P = 0.05$ according to Duncan's multiple-range test.

† Soil (500 g) containing 100 eggs and J2/g was placed at the specified depth in each hole on 12 May, and potatoes were harvested on 20 October 1988.

‡ Infection index: number of infected tubers per infection class × infection rating ÷ total number of tubers per hill; based on infection rating where 0 = 0 sites, 1 = 1–10, 2 = 11–25, 3 = 26–50, 4 = 51–75, 5 = 76–100, and 6 = 200+ infection sites per tuber.

§ Tubers with six or more infection sites were graded as culls.

DISCUSSION

Seasonal migration studies indicated that a portion of the *M. chitwoodi* population migrates downward during the winter and summer. This behavior may help nema-

TABLE 7. *Meloidogyne chitwoodi* second-stage juveniles (J2) recovered from soil samples taken from profiles of target hills in plots with nematodes placed at different depths 6 months earlier, Hermiston, Oregon.

Placement depth (cm)†	J2 (no./250 cm³ soil)				
	Around tubers	0–30 cm	30–60 cm	60–90 cm	90–120 cm
0	181 a	65 a	181 ab	0 a	0 b
30	73 a	165 a	399 a	23 a	0 b
60	145 a	17 ab	25 b	3 a	0 b
90	5 a	2 b	15 b	17 a	12 a
120	30 a	10 b	13 b	2 a	0 b

Values are means of five replicates. Means within a column followed by the same letter do not differ at $P = 0.05$ according to Duncan's multiple-range test.

† Soil (500 g) containing 100 eggs and J2/g was placed at the specified depth in each hole on 12 May, and soil samples were collected on 20 October 1988.

TABLE 8. Vertical migration of *Meloidogyne chitwoodi* after 9 days in tubes filled with soils† collected from Prosser, Washington, and Hermiston, Oregon.

Distance from inoculum (cm)	Nematodes detected (Mean ± SE)	
	Hermiston	Prosser
60	5 ± 3	0 ± 0
50	17 ± 7	0 ± 0
40	36 ± 12	0 ± 0
30	8 ± 4	0 ± 0
20	7 ± 4	1 ± 0.5
10	6 ± 2	13 ± 12
0‡	50 ± 32	189 ± 89

Values are the means of four replicates and represent the number of *M. chitwoodi* detected in tomato roots after a bioassay period of 3 weeks.

† Soil type: Hermiston, loamy sand; Prosser, sandy loam.

‡ *M. chitwoodi* J2 (5,000) were injected through a port in this bottom ring.

todes survive unfavorable environmental conditions. Some nematodes were able to survive in the top rings (5 cm deep) which were repeatedly subjected to freezing temperature during the 7-month period. This suggests that *M. chitwoodi,* like *M. hapla* (3), is able to survive subfreezing temperatures. Acclimation and migration to greater depths will ensure the persistence of *M. chitwoodi* through the winter. Similarly, in the summer trial, a few nematodes migrated downward and the rest, in the two top rings of the inoculum chambers, probably perished because of high temperature during the test period. Thus, migration may play an important role in survival and host finding by *M. chitwoodi.* Environmental conditions that favor migration, especially downward during the winter, need further investigation.

Upward migration of *M. chitwoodi* in the columns during the growing season was probably a response to irrigation water which was applied regularly. Earlier studies demonstrated that *M. chitwoodi* migrates upward in soil columns in response to water percolation (13). This apparent rheotaxis of root-knot nematodes is well adapted to potato production in the Pacific Northwest. Irrigation is not started until about 3 or 4 weeks after planting. Consequently, when nematodes deep in the soil migrate upward, a well-developed root system will be available before they reach the root zone. Our field observations indicated that the roots of potato penetrated to a depth of 40–45 cm. Hence, nematodes placed at 120 cm would have had to migrate 75–80 cm to encounter a food source.

Similar to results of previous studies (13), only a small fraction of the *M. chitwoodi* J2 population migrated upward and remained infective. However, this was sufficient to cause significant damage to potato tubers in field plots. Oregon and Washington inspectors would have downgraded or rejected lots of potatoes based on the percentage of culls due to internal defects caused by the nematodes or other factors, where 0–5% = U.S. number 1; 6–10% = number 2; and 11% or more = culls. The low preplant damage threshold of *M. chitwoodi* on potato (less than one egg/250 cm^3 soil (17)) reveals the importance of the migrating fraction of *M. chitwoodi.* However, the ability of *M. chitwoodi* to migrate and cause damage appears to depend on soil texture. At Hermiston, 100 and 10 eggs and J2/g soil placed at all depths (0–120 cm) were able to cause tuber damage in 1988 and 1989, whereas at Prosser, no tuber damage was observed at 90 or 120 cm. A difference between the suitability of soil for movement at the two sites was confirmed in soil tubes in the laboratory. The Prosser soil contained a much higher silt content (44–55%) than the Hermiston soil (16–17%). Prot and Van Gundy (14) indicated that the addition of silt and clay to sand may hinder the motility of root-knot nematodes in soil columns.

The final population of *M. chitwoodi* placed 0 and 30 cm deep was higher at Prosser than at the Hermiston site. At Hermiston, potato vines died earlier and root systems deteriorated earlier than at the Prosser site. Thus, the higher nematode population in the Prosser plots was most likely due to root systems that remained healthy for a longer period in the soil.

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