

Winter Survival of *Pratylenchus scribneri*¹

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Abstract: Population densities of *Pratylenchus scribneri* in a Plainfield loamy sand soil were sampled from 1 October to 1 May for 4 years. From May to October of each year, the site was planted to Russet Burbank potato and Wis 4763 corn. Percentages of change in population densities of nematodes were computed on the basis of number of nematodes present on 1 October. The decline of *P. scribneri* between growing seasons was nonlinear, with most mortality occurring in the autumn before the soil froze. Winter survival, defined as the percentage of change in population densities from 1 October to 1 May the following year, ranged from 50 to 136% for nematodes in corn plots and from 15 to 86% for nematodes in potato plots. There was no difference in survival of nematodes of different life stages or among root and soil habitats. Winter survival of nematodes was density-dependent in 3 of 4 years in corn plots and in 1 of 4 years in potato plots. Although predators were present, their abundance was not correlated with the winter survival of nematodes. Cumulative and average snow cover was correlated with the survival of nematodes associated with corn but not with potato. No relationships between other climatic factors and survivorship were detected.

Key words: cold tolerance, corn, extraction efficiency, overwintering, potato, *Pratylenchus scribneri*, lesion nematode, *Solanum tuberosum*, survival, *Zea mays*.

Population densities of *Pratylenchus* spp. usually decline between growing seasons in regions with harsh winters. Estimates of winter mortality for *P. penetrans* (Cobb) Filipjev & Schuurmans Stekhoven range from 33 to 68% (8,13). Significant decline in the density of *P. scribneri* Steiner in the winter of 1983 was reported from Iowa (12). Survival of *P. penetrans* was related to temperature (8) and moisture (7) in laboratory studies, but factors affecting winter survival of populations in the field are not understood.

Winter decline of nematodes in southern states where soil does not freeze can be great. Population densities of *Meloidogyne incognita* (Kofoid & White) Chitwood second-stage juveniles declined from 66 to 99% from October to April in Texas (15), from 13 to 80% from November to March in North Carolina (17), and up to ca. 90% during the winter in southern California (4). Winter survival for *M. incognita* varied with soil depth (15), location (4), and size of populations in the fall (4,15), but not with soil type (17).

Information on the rate and degree to which populations of nematodes decline during the winter months can be used to predict numbers of nematodes the next spring. If populations are small and likely to be below the detection level in the spring, estimates obtained in the autumn may be preferred for predicting potential crop loss. Decisions for managing nematodes are generally made in the autumn in areas where snow and frozen ground impede activity in fields in March and April.

The population dynamics of *P. scribneri* associated with corn and potato were determined from 1985 to 1989. Within the growing season, nematodes were primarily in roots, whereas in the autumn they were distributed about evenly between soil and root habitats (9). There was no evidence of vertical migration of *P. scribneri* following harvest (10).

The objectives of this study were to determine 1) the timing and extent of decline in populations from October to May, 2) variability in the decline of population densities from year to year, 3) whether survival varied among nematodes in different habitats or of different life stages, and 4) if the percentage of change in population densities was related to certain biotic and abiotic factors.

MATERIALS AND METHODS

Plots infested with *P. scribneri* were located at the Hancock Research Station,

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Plainfield, Wisconsin, on Plainfield loamy sand (92% sand, 5% silt, 3% clay; < 1% organic matter). During the summer, *Zea mays* L. cv. Wis 4763 and *Solanum tuberosum* L. cv. Russet Burbank were grown according to irrigation and production practices recommended for these crops in Wisconsin. Strips of corn and potato, eight rows wide and 93 m long, were staked along the row to demarcate 6-m-long plots. The plots were separated from each other by 3-m-long sections which were planted but not sampled. Corn and potato crops were adjacent but separated by a 3-m-wide fallow alley. The crops were planted and sectioned for sampling purposes in the same location every year, but in some years the crops were alternated so that corn followed potato and vice versa. Potato crops were harvested 1 October 1985, 30 September 1986, 2 October 1987, and 28 September 1988. There was no autumn tillage or cover crop planted in potato plots from 1985 to 1987, but rye was planted in October 1988. Corn crops were harvested 11 October 1985, 22 October 1986, 15 October 1987, and 3 October 1988. There was no tillage in the corn plots in the autumn of 1985, 1986, and 1988, but in 1987 plots were plowed on 10 November. In all years, plots were moldboard plowed in the spring between 8 April and 16 April and planted between 29 April and 8 May.

Soil samples were collected on, or shortly before, October 1 of each year before potatoes were harvested, twice thereafter before the soil froze, once no more than 10 days after soil thawed (before plowing), and once between 29 April and 3 May immediately before planting potatoes. The borders of the plots remained constant; each plot was considered to be one replicate, and six replicate plots were sampled for each crop. In each plot, six (1985, 1986) or ten (1987, 1988) 2.5-cm-d soil cores were collected with a sampling tube from the six inner rows to a depth of 45 cm in 1985, 37.5 cm in 1986 and 1987, and 30 cm in 1988. Four additional 6-m-long plots were included in the study in 1985 and 1986, but are not included in the data analyses

reported here. From 1985 to 1987, the cores were divided according to position in the vertical soil profile (three strata in 1985 and five strata in 1986 and 1987). All cores, or depth subsamples collected within a plot were composited to make one sample per sampling depth per plot. Nematode data for the different sampling depths included in the study during 1986 and 1987 are reported elsewhere (10).

From 1985 to 1987, soil samples were also collected in January when soil was frozen. Borders of plots were marked with tall stakes in the autumn to aid sampling under snow cover. Snow was removed with a shovel from at least three sites in each plot until bare ground was exposed. A soil core was removed to a depth of 15 cm from each site with an auger designed for sampling frozen soil (Oakfield Apparatus, Oakfield, WI). Cores from all sites within a plot were combined into a single sample.

A 100-cm³ portion of soil from each sample was processed by a centrifugal-flotation technique (6) using nested 250- μ m-pore and 38- μ m-pore sieves. Roots retained on the 250- μ m-pore sieve during the soil extraction procedure were incubated on Baermann funnels for 2 days at 24 C. Numbers of live *P. scribneri* per life stage were counted with a dissecting microscope; counts were adjusted for recovery efficiency (9). The life stages were distinguished by body length and the position of the genital primordium. Preliminary studies were conducted to correlate the appearance of the genital primordium in stained specimens viewed at 1,000 \times with a compound microscope with those same features in live specimens viewed at 375 \times with a stereomicroscope. A nematode was considered alive if movement was observed or if its body contents were forcefully expelled when the cuticle was ruptured. Unless stated otherwise, counts of nematodes recovered from the soil and root assays were added together to obtain a single estimate of nematode density per 100 cm³ soil. Tardigrades and predatory nematodes (Mononchidae) recovered during the soil assay procedure were also counted.

To determine if the rate of root egress on the Baermann funnels varied for nematodes recovered at different times during the winter, root samples were incubated for 7 days on 3 and 17 November 1987 and 2 February, 30 April, and 27 May 1988. The number of *P. scribneri* recovered after 2 days was divided by the cumulative number recovered after 7 days. Recovery percentages were compared among dates by analysis of variance.

For this study, counts of nematodes from different sampling strata were averaged for each plot to obtain a single estimate of population densities occurring within the top 30 cm of soil. Each 6-m plot was considered to constitute one replicate for data analyses. Mean counts for a single sampling date were computed using estimates from each of the six replicate plots sampled. Percentage of change (i.e., survival) within each plot was computed by dividing counts obtained from a plot by counts obtained from the same plot on or near 1 October. The average percentage of change for all plots was computed using the individual estimates of percentage of change from all six plots. To be consistent with established terminology (4), winter survival is denoted by $Pi2/Pf1$ where $Pi2$ = number of nematodes per 100 cm³ soil present on or near 1 May and $Pf1$ = number present the preceding autumn, on or near 1 October. Winter survival of *P. scribneri* was compared among years for each crop and among crops for each year by the SAS GLM procedure (14). Survival of nematodes in roots versus soil was evaluated for each crop within each year by plotting \ln (percentage of change) against \ln (time) and comparing the slopes fitted for data from each habitat. Survival of nematodes was correlated with counts of tardigrades and Mononchid nematodes and weather data collected near the study site at the Hancock Research Station. Climatological data included daily mean, minimum, and maximum soil temperature at 12 cm, rainfall and snowfall, and snow cover. Soil moisture was determined in the fall and spring for 2 years, but the practice was discontinued because

TABLE 1. Winter survival of *Pratylenchus scribneri* in corn and potato plots, 1985–89.

	Initial density (Pf1)†		Survival (Pi2/Pf1)†	
	Corn	Potato	Corn	Potato
1985–86	429 a	371 a	1.36 a	0.85 a
1986–87	1,088 b	528 a*	0.37 b	0.23 b*
1987–88	1,313 b	747 a	0.50 b	0.16 b*
1988–89	1,343 b	268 a*	0.37 b	0.36 ab

Data are the means of six replications. Means within a column followed by the same letter are not different ($P \leq 0.05$) according to Duncan's multiple-range test.

* Denotes significant ($P \leq 0.05$) differences among corn and potato for that parameter.

† Pf1 refers to populations present 1 October; Pi2 refers to populations present 1 May.

the sandy soil was well drained and moisture content was consistent among dates. Counts of life stages were transformed using \ln values and analyzed by analysis of variance.

RESULTS

Population densities of *P. scribneri* declined from October to May in potato plots from 1985 to 1988 and in corn plots from 1986 to 1988 (Table 1). In 1985, population densities increased during the winter in corn plots. Estimates of winter decline varied among crops for 2 of the 4 years of the study. For each crop, survival of *P. scribneri* was higher in 1985 than in the other 3 years.

Winter survival of nematodes in potato plots was not related to the climatological factors in Table 2. Winter survival of *P. scribneri* in corn plots was positively correlated ($r = 0.97$, $P = 0.001$) with the mean and cumulative snow cover for the winter, but not with other climatological factors. In general, however, there was a trend for a positive relationship between the monthly average soil temperature and survival. Ambient temperature (not presented) was variable, particularly during January and February (e.g., range = -12 to 4 C for January 1986), and was not correlated with the survival of nematodes.

Survival of *P. scribneri* ($Pi2/Pf1$) was negatively correlated with transformed counts of nematodes present on 1 October in corn plots in 1985 ($r = -0.92$, $P = 0.01$), 1986

TABLE 2. Winter soil temperature (C) at 12 cm and precipitation (cm) data collected daily at the Hancock Research Station, 1 km from the study site.

	1985-86	1986-87	1987-88	1988-89
		Minimum temperature (C)		
1 Oct-freeze†	12.5	11.8	8.7	8.4
1 Oct-1 May	4.7	4.6	4.0	4.0
		Maximum temperature (C)		
1 Oct-freeze	14.0	15.0	12.3	12.0
1 Oct-1 May	5.8	6.3	7.0	6.2
		Average temperature (C)		
October	17.0	17.1	18.9	19.4
November	13.1	11.9	9.4	10.3
December	0.6	0.4	1.3	0.6
January	-0.7	0.1	-0.4	-0.7
February	-0.6	-0.1	-0.9	0.0
March	0.4	1.2	0.8	0.0
April	9.5	5.9	9.0	6.8
		Cumulative rainfall (cm)		
1 Oct-freeze	23	33	21	26
1 Oct-1 May	44	47	36	35
No. rain events \geq 0.25 cm	41	32	37	34
No. days frozen	74	98	74	108
Average snow cover (cm)	30	6	14	6
Cumulative snow cover (cm)	199	116	144	136
Date soil froze	7 Nov	11 Nov	7 Dec	12 Dec
Date of first snow cover	22 Nov	18 Nov	25 Nov	6 Nov

Unless otherwise specified, data refer to period 1 October-1 May.

† 1 October until first day soil froze.

($r = -0.98$, $P = 0.03$), and 1987 ($r = -0.93$, $P = 0.01$) and in potato plots in 1987 ($r = -0.82$, $P = 0.04$). Mean population densities of tardigrades and Mononchid nematodes averaged from 1 October to 1 May

ranged from 0 to 3 and 2 to 5 per 100 cm³ soil, respectively, and were not correlated with the percentage of change in populations of *P. scribneri*.

Mean percentage of change in population densities of *P. scribneri* fluctuated among sampling dates (Fig. 1). A general survival function was generated by plotting $\ln(Pi2/Pf1)$ values from corn and potato plots for 1986 to 1988 against $\ln(\text{days after 1 September})$. The rate at which populations declined was nonlinear ($\ln[Pi2/Pf1] = 2.10 - 0.591 \ln[x]$), with most change occurring in the autumn. In 1986 and 1987, counts of nematodes did not differ between samples collected before soil freezing in the autumn and those collected the day of planting the next spring. Population densities increased ($P \leq 0.05$) in the autumn in corn plots in 1985 and 1987 and in potato plots in 1985. In 1985, *P. scribneri* increased ($P \leq 0.05$) in corn plots from April to May.

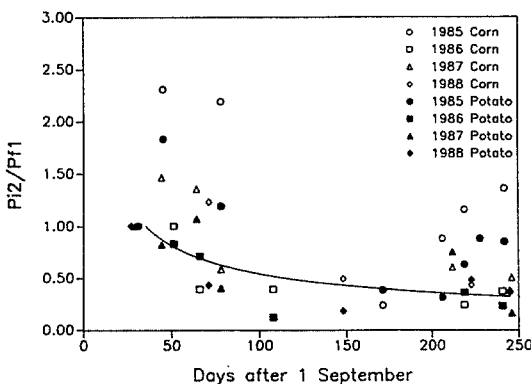


FIG. 1. Average percentages of change in populations of *Pratylenchus scribneri* recovered during the winters of 1985 to 1989 in plots cropped to corn and potato in the summer. A survival function ($\ln[Pi2/Pf1] = 2.10 - 0.591 \ln[x]$, $r^2 = 0.32$, $P \leq 0.05$) was computed with data from 1986 to 1988.

TABLE 3. Winter survival (Pi2/Pf1) of *P. scribneri* in roots and soil in corn and potato plots, 1985-89.

	Potato		Corn	
	Roots	Soil	Roots	Soil
1985-86	1.08 a	0.69 a	1.39 a	1.34 a
1986-87	0.22 b	0.30 a	0.35 b	0.44 a
1987-88	0.21 b	0.13 b	0.67 b	0.38 b
1988-89	0.50 b	0.24 a	0.46 b	0.15 b

Data are the means of six replications. Means within a column followed by the same letter are not different ($P \leq 0.05$) according to Duncan's multiple-range test.

Separate estimates of the change in population densities in soil and root fractions of the samples also varied among years (Table 3). Slopes of lines fitted to ln values for the percentage of change in population densities recovered from roots and soil were not different for either corn or potato in any year (data not presented).

On 1 October, populations (Pf1) were comprised primarily of juveniles (Table 4). Of the juvenile life stages, fourth-stage juveniles tended to predominate. Numbers

of all stages declined during the winters of 1986 to 1988. There was no difference in the mean winter survival (Pi2/Pf1) among the life stages.

No differences in the percentages of recovery of *P. scribneri* by the Baermann extraction procedures after 2 days were detected among dates. Mean percentage of recovery of all life stages from roots incubated for 2 days was 50%, 51%, 52%, 48%, and 43% of that collected after 7 days on 3 November, 17 November 1987, 2 February, 30 April, and 27 May 1988, respectively.

Data from samples collected in January were not representative of data collected on other dates. Soil samples were very wet after thawing at room temperature, making it difficult to obtain an aliquot that was standard, either volumetrically or gravimetrically, with aliquots processed on other dates. Live nematodes were recovered when frozen soil was sampled to a depth of 15 cm, but fewer nematodes were re-

TABLE 4. *Pratylenchus scribneri* per 100 cm³ soil by life stage in corn and potato plots on 1 October (Pf1) and 1 May (Pi2) 1985-89.

Life stage	Potato			Corn		
	Pf1	Pi2	Pi2/Pf1	Pf1	Pi2	Pi2/Pf1
1985						
J2	66 a	73 a	1.98 a	53 a	114 a	3.57 a
J3	75 a	24 a	0.92 a	108 a	118 a	1.45 a
J4	118 a	37 a	0.58 a	205 a	129 a	1.05 a
A	112 a	44 a	0.54 a	63 a	19 b	1.19 a
1986						
J2	86 ab	32 a	0.35 a	407 a	96 a	0.38 a
J3	131 a	32 a	0.23 a	424 a	112 a	0.32 a
J4	251 c	59 b	0.23 a	197 a	88 a	0.50 a
A	61 b	9 b	0.17 a	60 b	15 b	0.33 a
1987						
J2	236 a	12 a	0.60 a	328 a	143 a	0.61 a
J3	217 a	31 b	0.21 a	383 a	220 b	0.69 a
J4	255 a	38 b	0.16 a	493 a	88 c	0.38 a
A	39 b	6 a	0.23 a	109 b	35 d	0.34 a
1988						
J2	75 a	16 a	0.24 a	443 a	253 a	0.56 a
J3	68 a	25 a	0.44 a	446 a	174 ab	0.42 a
J4	99 a	25 a	0.45 a	345 a	71 b	0.16 a
A	25 a	4 a	0.24 a	109 b	17 c	0.26 a

Means within a column and year followed by the same letter are not different ($P \leq 0.05$) according to Duncan's multiple-range test. Mean separation of Pf1 and Pi2 data, but not Pi2/Pf1, was computed with transformed ($\ln[x]$) data. Pi2/Pf1 values were calculated from Pi2 and Pf1 values of individual replications, not from mean Pi2 and Pf1 values listed in the table.

covered than when samples were collected to a depth of 30 cm either before freezing or after thaw.

DISCUSSION

The winter decline in population densities of *P. scribneri* associated with corn ranged from 50 to 63% and was similar to reductions reported for field populations of *P. penetrans* associated with red clover (43–68% decline) (8) and rye (40–65% decline) (13) in Canada. For potato, the winter survival of *P. scribneri* was more variable, ranging from 15 to 84%, and lower than that estimated for corn in 2 of 4 years. Although the winter survival of *Pratylenchus* spp. may vary between these crops or between cropped and fallow land (13), the possibility that populations were redistributed, and hence estimates decreased, when potatoes were harvested cannot be discounted.

In 2 of 4 years, the winter decline in numbers of *P. scribneri* occurred exclusively in the autumn before the soil froze. In the other years, the decline and freezing of the soil both occurred between sample dates and it was not possible to determine if the decline preceded freezing. Temporal variation in the decline of populations between growing seasons was as great as the increase of the same populations during the growing season (10). Because this variability may apply to other systems, caution is warranted when differences in survivorship are compared among locations and years.

In this study and in one of the Canadian studies (8), population densities were greater at planting than in the autumn in 1 of 4 years. Our data indicate that high winter survival was due, in part, to an increase in population densities from October to November. No seasonal vertical migration of nematodes was detected for our population (10), so the increase in population densities in spring was probably not due to emigration. It is also unlikely, on the basis of evaluations of our root assay procedure, that there was a discrepancy in our recovery procedures and hence counts of

nematodes among sampling dates. A more likely explanation is that counts of second-stage juveniles were increased in the autumn after 1 October or in the spring by a greater than average hatch of eggs, a life stage not included in estimates of population densities. Findings that juveniles of *P. scribneri* increased between plowing and planting (11) and that second-stage juveniles of *P. penetrans* increased from January to April (3) were also interpreted as evidence of natality. Although egg hatch occurring in autumn and spring undoubtedly affects estimates of the winter survival of *Pratylenchus* spp., all studies with *Pratylenchus* spp. to date show that mortality is usually greater than natality during the winter.

Weather data of the type generally available to farmers were not useful for predicting the winter survival of *P. scribneri* in this study. Laboratory studies with *P. penetrans* (Forge, unpubl.) and *Meloidogyne hapla* (5) recovered close to the study site show that mortality can be induced by temperatures above the freezing point of soil moisture. On the basis of studies in controlled environments (7,8,16), there is little doubt that *P. penetrans* is susceptible to freezing. The failure of this study to detect relationships of temperature and precipitation to the survival of *P. scribneri* could result from data collected at an inappropriate scale or a data set that was too small.

The correlation of winter survival of nematodes in corn plots with snow cover is indirect evidence that abiotic factors do affect nematode population densities during the winter. This finding supports observations (8) and evidence from experimental plots where snow was removed (1,11) that survival of nematodes is higher under snow than in bare ground. In our study, it is more likely that snow cover affected soil moisture rather than temperature, since soil froze with or without snow cover and little mortality appeared to occur after the soil froze regardless of snow cover.

For some data sets, the relationship between percentage of change in the popu-

lation of *P. scribneri* was dependent on nematode density in the autumn. Similar relationships between the size of populations of *Meloidogyne incognita* and winter survival have been attributed to biotic factors (4) and temporal variation in the partitioning of host reserves, and thus the viability of nematodes (15). The latter hypothesis may be relevant for *P. scribneri* in this study, since two known predators, tardigrades and Mononchid nematodes, had no apparent effects on survival and population densities of *P. scribneri* were large in the fall when hosts were declining.

Our data for *P. scribneri* support some studies of *P. penetrans*, but not others, in defining whether certain segments of a population are more likely than others to survive between growing seasons. Our data are in agreement with Dunn (3) in that there was no difference in the rate at which population densities declined in root or soil habitats. Whether the data were confounded by movement of nematodes between roots and soil is unclear because of a lack of information about the behavior and mobility of *P. scribneri* at low temperature. In contrast to reports (2,11) that adults and fourth-stage juveniles were the most abundant overwintering stages of *P. penetrans*, we found that, although these stages tended to be the most abundant in the fall, all life stages survived equally well.

Though the exact causes of nematode mortality during winter have not been identified for any crop system, many factors may contribute to the decline of populations. The importance of field studies is to determine the likelihood that these factors actually regulate the winter survival of nematodes and if so, to provide information useful for predicting the decline of populations. Establishing when mortality occurs and characterizing the members of a population that die are important for directing and interpreting studies on the effects of specific factors capable of killing nematodes.

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