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INTEGRATED PEST MANAGEMENT

Nematode Population Changes under Crop Rotation Sequences: Consequences for Potato Production

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ABSTRACT

Soils of the Klamath basin of northeast California and southeast Oregon that are used for a potato (*Solanum tuberosum* L.) cropping system are frequently infested with *Meloidogyne chitwoodi* (Golden, O'Bannon, Santo & Finley) and *Pratylenchus neglectus* (Filipjev & Schuurmans-Stekhoven). These studies were conducted over a 7-yr period to determine nematode population changes under crop rotation sequences, and the impact of those changes on potato crop yield and quality. The surface blemish rating of a summer-grown potato crop has a log-linear relationship with the population level of *M. chitwoodi* measured either the previous fall, or with lower reliability, in the spring before potato planting. Yield of Grade no. 1 potato was negatively related to population levels of *M. chitwoodi* measured the previous fall, although total yields were not affected. On crops that are hosts to *M. chitwoodi* or *P. neglectus*, seasonal multiplication rates of the nematodes were log-linearly related to populations measured the previous fall. The relationship between crop yields, or nematode multiplication rates, and spring nematode population levels were weaker due to the imprecision of spring population assessments. Overwinter survival rates of both nematode species were log-linearly related to population levels measured in the fall. Preliminary analysis of the impact of seasonal climatic variation suggests that the models may underpredict potato tuber blemish and nematode population increase one year in five, when higher soil temperatures prevail. The predictions of crop damage and nematode population change allow crop and nematode management decisions based on population assessment.

THE COLUMBIA ROOT-KNOT NEMATODE, *Meloidogyne chitwoodi*, is a major pest of potato in Colorado, Idaho, Utah, Washington, and the Klamath Basin of northeast California and southeast Oregon (Nyczepir et al., 1982; Pinkerton and McIntyre, 1987; Santo et al., 1980). *Meloidogyne chitwoodi* was first described in 1980 (Santo et al., 1980), but specimens from the Klamath Basin deposited in the nematode collection of the California Department of Food and Agriculture in the mid-1960s suggest that the nematode was previously designated as *M. thamesi* (R.W. Hackney and A.C. Weiner, personal communication). Another nematode species in the cropping system, *Pratylenchus neglectus*, could become important if it were to increase in prevalence (Ferris et al., 1993; Siddiqui et al., 1973; Umesh and Ferris, 1992).

Approximately 9300 ha of Russet Burbank potato are grown in the Klamath Basin, primarily for the fresh market. The latitude (42° N) and altitude (1250 m above sea level) of the high desert region create a 120-d growing season, with warm days and cool nights. Frost can occur on any night during the growing season. Conditions become suitable for soil tillage and planting in mid-May, and the potato crop is usually harvested by early October.

Field experiments show little evidence of yield reduction caused by the direct effect of the nematode population on potato crop growth (Griffin, 1985; Pinkerton and Santo, 1986). The major damage to potato tubers is a nematode-induced blemish, which lowers or negates tuber marketability. When 10% or more of the tubers are blemished, the crop is usually unmarketable.

Nematode damage is caused by the second and third generation of *M. chitwoodi* in a given growing season. The overwintering population penetrates roots, develops, and starts to produce eggs about 650 accumulated degree-days above a basal threshold of 5°C (DD_5) after planting. Second-stage juveniles of the second generation penetrate roots and bulking tubers commencing about 950 DD_5 after planting, although very young tubers may be resistant or unattractive to the nematodes due to toxic metabolites and closed lenticels (Inserra et al., 1983; Pinkerton et al., 1986). A third generation of infective juveniles may be produced if soil temperatures exceed 2000 DD_5, resulting in further invasion of the tubers (Griffin, 1985). In areas with greater seasonal DD_5 accumulations and longer growing seasons, such as the Columbia River Basin of Washington, four or five field generations may be possible.

It requires only a few second-stage juveniles in the overwintering population to produce substantial second- and third-generation population levels. Thus, the economic threshold for tuber blemish may be at or below the limit of detection when the *M. chitwoodi* population is measured in the spring. The nematode population is probably best measured in the fall, at the end of the previous crop. Individuals are more abundant then, and there is more time available for sample processing and management decisions (Ferris, 1985).

The availability and acceptability of nematicide options for nematode management are diminishing. Further, much of the soil in the Klamath Basin region is an unclassified silty clay loam with 12% organic matter content. Nematicide efficacy on this soil has been poor or inconsistent (Westerdahl et al., 1992).

One management tactic for the Columbia root-knot nematode is the use of nonhost or resistant crops in the rotation. Alternate crops have been investigated for infested regions throughout the Pacific Northwest (Ferris et al.,

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Abbreviations: DD_5, degree-day threshold of 5°C; P, population density. *Subscripts:* f, fall (current crop, equivalent to f2 subscript); f1, previous fall (after harvest of previous crop); f2, harvest fall (after harvest of current crop); i, spring (before planting current crop); i2, next spring (before planting next crop); t, tolerance level.

1993; Griffin, 1991; Mojtahedi et al., 1991; Griffin and Asay, 1989; Santo and Ponti, 1985; Santo et al., 1988). Principal rotation crops in the Klamath Basin are alfalfa (*Medicago sativa* L.) and barley (*Hordeum vulgare* L.). Although economically questionable for the cropping system, especially in short-term rotations, both crops are used for agronomic benefits to the soil. Unfortunately, barley is a host of the Columbia root-knot nematode, and alfalfa, although a nonhost to the prevalent biotype (Race 1) of the Columbia root-knot nematode, is a host to a second biotype (Race 2) and to *M. hapla* (Mojtahedi et al., 1988; Santo and O'Bannon, 1981). Both crops are hosts of the lesion nematode, *P. neglectus*, which often co-occurs with *M. chitwoodi* (Griffin, 1991; Griffin and Gray, 1990; Mojtahedi and Santo, 1992; Umesh and Ferris, 1992). Sugar beet (*Beta vulgaris* L.), which is being introduced into the area, is a host of *M. chitwoodi* (Ferris et al., 1993).

Our objectives were to determine nematode population changes under crop rotation sequences and the impact of those changes on potato crop yield and quality.

MATERIALS AND METHODS

A 7-yr experiment, initiated in 1985, investigated crops that are conventionally grown in the Klamath Basin area for their potential as rotation crops in fields infested with the Columbia root-knot nematode. Eight replications of 7-row plots, 6.5 by 15.25 m, were arranged in a randomized complete block design. Nematode population and plant growth data were collected from the center 3.65- by 12.2-m area. The rotation sequence commenced in 1982 and extensive nematode monitoring was initiated in the plots in 1985. All plots were in potato in 1982 and in barley in 1983. Rotation crops in 1984 were alfalfa, barley, onion (*Allium cepa* L.), and potato (Table 1). In 1988, four rotation sequences were split and maintained as four replications of each for the remainder of the experiment.

Ten cropping sequences were included in the experiment. Original larger plots were split and either treated or not treated with the fumigant nematicide 1,3-dichloropropene in the fall of 1985. The whole experiment was cropped uniformly to potato in 3 of those 7 yr, and uniformly to barley once. The crops used in the various rotation sequences were alfalfa, barley, potato, and a weed-free summer fallow (Table 1).

Data Collection and Analysis

Population levels of *M. chitwoodi* and *P. neglectus* were assessed before planting and immediately post harvest. Population assessment for each plot at each sampling period was based on two composite samples each of 12 soil cores, 2.5 cm diam. and 30 cm deep. Soil samples were hand-mixed and nematodes were extracted from a 350-cm^3 subsample. A semiautomatic elutriator was used to separate the subsample into a root and organic matter fraction retained on a 40-mesh (367-μm opening) sieve and a fraction retained on a 400-mesh (38-μm opening) sieve. The root and organic matter fraction was placed in a mist chamber for 5 d to allow egg hatch and emergence of motile endoparasitic stages. The latter fraction was subjected to sugar-centrifugation in 1-molar sucrose solution (Byrd et al., 1976). Population levels of *M. chitwoodi* and *P. neglectus* in each sample were expressed per 1000 cm^3 soil as the sum of the individuals detected in the sugar-centrifuge and mist chamber fractions. Population levels per plot were calculated as the average of the two samples from each plot.

Table 1. Crop rotation sequences completed in the 64 plots of an experiment investigating the effect of rotation on nematode population.

	Rotation sequences†							
Reps	1984	1985	1986	1987	1988	1989	1990	1991
8	O	F+‡	P	P	F	P	B	P
8	O	F−	P	P	F	P	B	P
8	O	P+	P	P	F	P	B	P
8	O	P−	P	P	F	P	B	P
8	B	F+	P	F	P	P	B	P
8	B	F−	P	F	P	P	B	P
8	B	P+	P	F	P	P	B	P
8	B	P−	P	F	P	P	B	P
8	A	F+	P	A	A	P	B	P
8	A	F−	P	A	A	P	B	P
8	A	A+	P	A	A	P	B	P
8	A	A−	P	A	A	P	B	P
4§	P	B+	P	B	B	P	B	P
4	P	B−	P	B	B	P	B	P
4	P	B+	P	B	P	P	B	P
4	P	B−	P	B	P	P	B	P
4	P	F+	P	B	B	P	B	P
4	P	F−	P	B	B	P	B	P
4	P	F+	P	B	P	P	B	P
4	P	F−	P	B	P	P	B	P

† O = onion; A = alfalfa; B = barley; F = fallow; P = potato.

‡ Plus (+) or minus (−) indicates 1,3-dichloropropene nematicide applied or not applied in fall 1985.

§ Cropping sequences were split in 1988 and maintained as four replications through 1991.

Tuber yields were measured on all potato crops, and potato tubers were evaluated for nematode-induced surface blemishes in accordance with USDA fresh-market potato grading standards. Field observations and companion trials showed little impact of either nematode species on growth of the rotation crops (e.g., Umesh and Ferris, 1992, 1994; Ferris et al., 1993), so their yields were not measured.

Seasonal Multiplication Rates

Seasonal multiplication rates in relation to population density, P_f/P_i, for both *M. chitwoodi* and *P. neglectus* on alfalfa, barley, fallow, and potato were determined on an individual-season basis, and averaged across several seasons. Data were smoothed by averaging the P_f/P_i values for ln 0.5 increments of P_i values. This smoothing revealed the underlying nature of the relationship to allow selection of appropriate models (Ferris, 1984). We recognize that there may be a tolerance level below which there is no impact of initial population density on nematode multiplication or survival, and above which there is a definable relationship based on host damage, diminished resources, antagonism, and other density-dependent effects. Essentially, our conceptual model has two parts, reflecting the change in the nature of the relationship at the tolerance level (e.g., Fig. 1a–d).

The fit of the models to datasets was measured by R^2 values calculated as $1 - [(\Sigma(o - p)^2)/(n - 2)]/[(\Sigma(o - m)^2)/(n - 1)]$ from the number (n) observed (o), predicted (p), and mean of the observed (m) values (Snedecor and Cochran, 1967). Analyses were conducted on both raw (nonsmoothed) and smoothed datasets. Only smoothed data are graphically presented, to allow evaluation of central trends; however, parameter values for both smoothed and raw datasets are provided in Tables 2 and 3. When smoothed datasets were subjected to regression analysis, each smoothed data point was weighted by the number of raw data points on which it is based. The significance of R^2 values was tested conservatively for the regressions on smoothed datasets by using probability levels for $n - 2$ smoothed points rather than for the number of underlying raw data points.

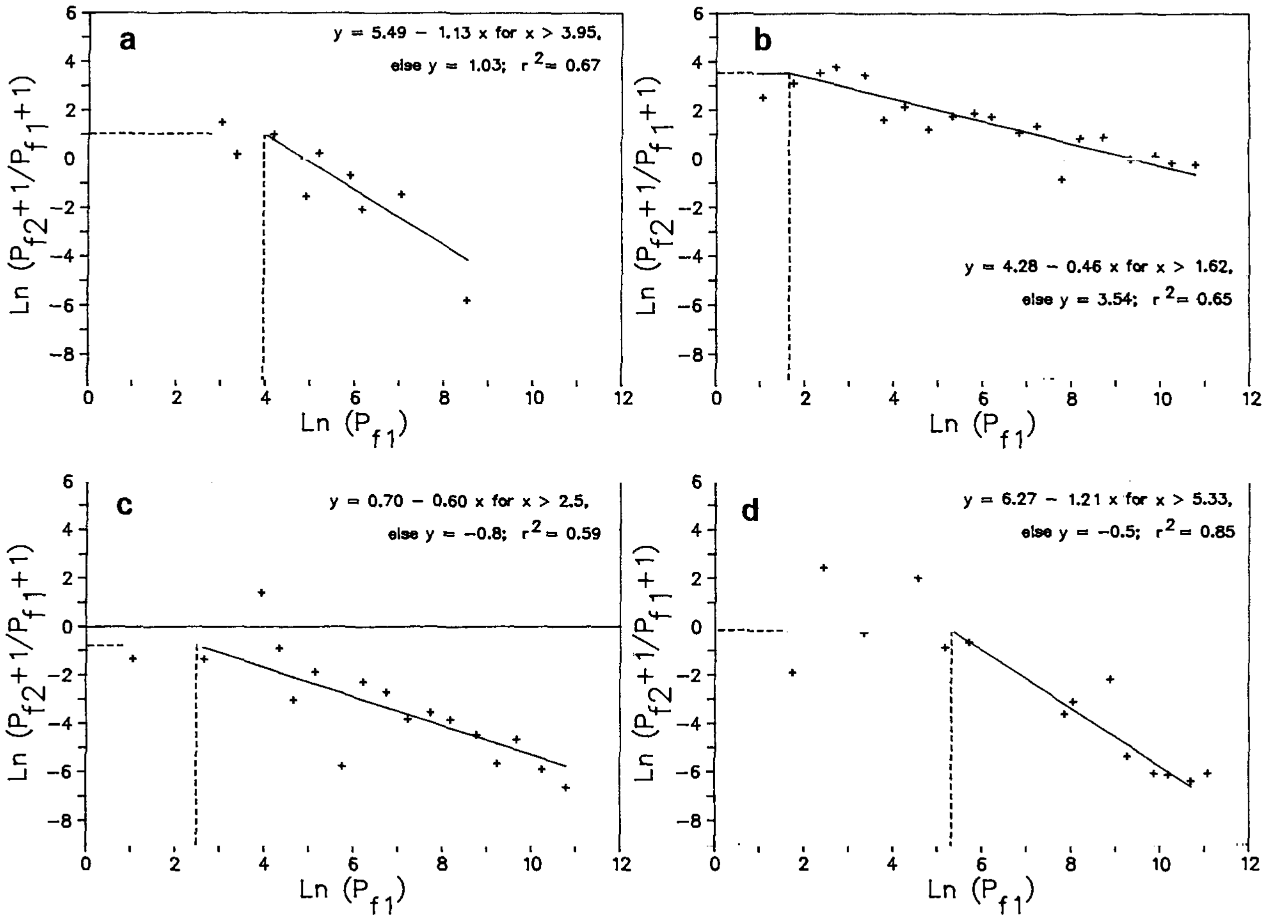

Fig. 1. Seasonal multiplication rates of *Meloidogyne chitwoodi* in relation to population levels assessed the previous fall: (a) alfalfa; (b) potato; (c) barley; (d) fallow.

The model was fitted to two datasets for both *M. chitwoodi* and *P. neglectus* on each crop:

$$\ln[(P_{f2}+1)/(P_{f1}+1)] = a - b(\ln P_{f1}), \quad \ln P_{f1} > X_t$$
$$= Y_t, \quad \ln P_{f1} \le X_t \qquad [1]$$

where P_{f2} is the population level following the crop of interest, P_{f1} is the population level the previous fall (i.e., following the previous crop), X_t is the ln value of the tolerance level estimated by visual observation of the plotted dataset. Y_t is the ln value of the nematode multiplication rate, the value of $\ln[(P_{f2}+1)/(P_{f1}+1)]$ when $\ln P_{f1} \le X_t$ (note: $Y_t = a$ when $X_t = 0$) (e.g., Fig. 1a–d). The parameters of the model are calculated by excluding data where $P_{f1} = 0$ to avoid bias created by nondetection of nematodes.

$$\ln[(P_f+1)/(P_i+1)] = a - b(\ln P_i), \quad \ln P_i > X_t$$
$$= Y_t, \quad \ln P_i \le X_t \qquad [2]$$

where P_f is the population level following the crop of interest (equivalent to P_{f1} in the previous model), P_i is the population level in the spring before planting, and other parameters are as for the previous equation. The parameters of the model are calculated by excluding data where $P_i = 0$.

Survival rates were determined in relation to population density in the absence of a host crop (summer fallow) on an individual-season basis and averaged across several seasons, using the same models as for seasonal multiplication.

Overwinter Survival Rates

Overwinter survival rates for both nematode species, $(P_{i2}+1)/(P_{f1}+1)$, where P_{f1} is the population measured in the fall (i.e., the final population after the previous crop), and P_{i2} is the population measured the following spring (i.e., the initial population for the next crop), were determined in relation to population density on an individual-winter basis and averaged across several winters. The model used was the same as that for seasonal multiplication rates (Fig. 1a–d), and datasets were smoothed by averaging ordinate values for ln 0.5 increments of abscissa values (Ferris, 1984).

Crop Yields in Relation to Nematode Population Densities

Potato crop yields (total tuber weight) were related to population densities of both *M. chitwoodi* and *P. neglectus* using one of two models:

$$\ln y = a - b(\ln P_i) \qquad [3]$$

or

$$\ln y = a - b(\ln P_{f1}) \qquad [4]$$

where y is the crop yield. In both cases, the model is fit to datasets for each crop in individual years, and for data averaged across

Table 2. Linear regression model parameters for population increase and decrease of *M. chitwoodi* (Mc) and *P. neglectus* (Pn) under a range of crops and conditions, based on number (*n*) in the previous fall (f) or spring (s) population assessments in crop rotation experiments conducted from 1985 to 1991.

Data	Treatment	Pop. assessment	Slope	*Y*-intercept	X_t†	Y_t‡	*n*	R^2	Pr§
sm¶	Mc-Potato	s	−0.17	2.94	0.0	2.94	16	0.18	NS
raw		s	−0.16	2.95	0.0	2.95	192	0.03	*
sm		f	−0.46	4.28	1.62	3.54	20	0.65	**
raw		f	−0.46	4.31	1.67	3.54	141	0.27	**
sm	Mc-Barley	s	−0.22	−1.00	0.0	−1.00	14	0.08	NS
raw		s	−0.15	−1.26	0.0	−1.26	84	0.01	NS
sm		f	−0.60	0.70	2.5	−0.80	17	0.59	**
raw		f	−0.62	0.81	2.61	−0.80	85	0.17	**
sm	Mc-Alfalfa	s	−1.01	5.21	4.10	1.07	9	0.83	**
raw		s	−0.98	5.03	4.05	1.07	29	0.35	**
sm		f	−1.13	5.49	3.95	1.03	9	0.67	**
raw		f	−1.11	5.38	3.92	1.03	27	0.38	**
sm	Mc-Fallow	s	−0.95	3.78	4.00	0.0	11	0.99	**
raw		s	−0.89	3.35	3.76	0.0	32	0.51	**
sm		f	−1.21	6.27	5.33	−0.50	14	0.85	**
raw		f	−1.19	6.09	5.27	−0.50	34	0.71	**
sm	Pn-Potato	s	−0.47	3.27	0.0	3.27	14	0.65	**
raw		s	−0.47	3.27	0.0	3.27	218	0.16	**
sm		f	−0.36	3.03	0.0	3.03	12	0.54	**
raw		f	−0.35	3.01	0.0	3.01	165	0.12	**
sm	Pn-Barley	s	−0.48	3.49	0.0	3.49	10	0.44	*
raw		s	−0.48	3.52	0.0	3.52	84	0.15	**
sm		f	−0.62	3.98	0.0	3.98	13	0.91	**
raw		f	−0.62	4.02	0.0	4.02	86	0.34	**
sm	Pn-Alfalfa	s	−0.40	1.96	0.0	1.96	8	0.42	NS
raw		s	−0.39	1.92	0.0	1.92	31	0.14	*
sm		f	−0.68	2.90	0.0	2.90	7	0.47	NS
raw		f	−0.63	2.60	0.0	2.60	30	0.15	*
sm	Pn-Fallow	s	−0.52	1.68	0.0	1.68	7	0.32	NS
raw		s	−0.51	1.61	0.0	1.61	32	0.11	NS
sm		f	−0.29	0.21	0.0	0.21	7	0.06	NS
raw		f	−0.37	0.67	0.0	0.67	32	0.03	NS
sm	Mc-Survival	f	−0.55	2.39	2.19	1.18	21	0.84	**
raw		f	−0.54	2.34	2.19	1.15	275	0.32	**
sm	Pn-Survival	f	−0.40	1.62	0.0	1.62	14	0.63	**
raw		f	−0.39	1.57	0.0	1.57	312	0.09	**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† ln value of the tolerance level.
‡ ln value of the maximum multiplication rate.
§ Probability that $R = 0$.
¶ sm = smoothed data, raw = raw data.

years. The datasets were smoothed by averaging ordinate values for ln 0.5 increments of abscissa values (Ferris, 1984).

Tuber Blemish Ratings

Regressions were determined for the relationship between tuber blemish rating in potato crops and the population density of *M. chitwoodi* measured in the spring (P_i) or the previous fall (P_{fl}) for individual years and averaged across years. The models used were:

$$\ln y = a - b(\ln P_i) \qquad [5]$$

$$\ln y = a - b(\ln P_{fl}) \qquad [6]$$

where y is the percentage of tubers with surface blemish. In both cases, the model is fit to datasets for each crop in individual years, and for data averaged across years. The datasets were smoothed by averaging ordinate values for ln 0.5 increments of abscissa values (Ferris, 1984).

Effect of Annual Climatic Variation on Population and Tuber Blemish

There are three component parameters of the linear relationships used in these studies. The tolerance level (X_t) is the population level at which the effects of increasing population density on plant growth or seasonal population change become apparent. The maximum multiplication rate (Y_t) is the average multiplication rate at population levels below the tolerance level. The slope of the regression line (b) for population levels greater than X_t indicates the impact per incremental increase in the nematode population density. The parameters are not independent for a dataset: if the maximum multiplication rate is high, the regression slope may be steep; if the tolerance level is low, the slope may be more gradual. Conceivably, all three parameters may be influenced by climatic conditions, and we expect that soil temperature is a major determinant. Due to the interdependence of the parameters, the area under the multiplication rate line was used as a measure of nematode population potential for a single growing season. For the same reasons, the area under the regression was used to determine the effect of seasonal climatic conditions on nematode overwinter survival data and potato tuber blemish.

Soil temperatures at the 15-cm depth were recorded at the nearby Intermountain Research and Extension Center in Tulelake, CA. Cumulative degree-days (base 5°C) were calculated from monthly average soil temperatures for the growing season (arbitrarily defined as 1 May to 30 September) for each year as a measure of heat units available to the nematode population.

Table 3. Linear regression model parameters for potato yield (total and Grade no. 1) and quality (blemish) in relation to population levels of *M. chitwoodi* (Mc) and *P. neglectus* (Pn), based on number (*n*) in the previous fall (f), fall after harvest (f1) or spring (s) population assessments in crop rotation experiments conducted from 1985 to 1991.

Data	Treatment	Pop. assessment	Slope	*Y*-intercept	X_t†	Y_t‡	*n*	R^2	Pr§
sm¶	Mc–Total yield	s	−0.011	10.47	0.0	10.47	16	0.38	**
raw		s	−0.011	10.45	0.0	10.45	165	0.02	NS
sm		f	0.01	10.56			23	0.11	NS
raw		f	0.00	10.41			165	0.001	NS
sm	Pn–Total yield	s	−0.03	10.58	0.0	10.58	13	0.77	**
raw		s	−0.04	10.58	0.0	10.58	165	0.20	**
sm		f	−0.04	10.63	0.0	10.63	14	0.59	**
raw		f	−0.04	10.63	0.0	10.63	165	0.15	**
sm	Mc–Yield no. 1	f	−0.055	10.47	2.5	10.33	18	0.80	**
raw		f	−0.054	10.46	2.4	10.33	153	0.32	**
sm	Pn–Yield no. 1	f	−0.015	10.29	0.0	10.29	16	0.14	NS
raw		f	−0.015	10.29	0.0	10.29	153	0.011	NS
sm	Mc–Blemish	s	0.32	0.91			14	0.38	*
raw		s	0.32	0.88			84	0.17	**
sm		f	0.34	0.64			16	0.72	**
raw		f	0.34	0.61			82	0.35	**
sm	Pn–Blemish	s	−0.04	2.80			12	0.02	NS
raw		s	−0.041	2.78			90	0.002	NS
sm		f	0.23	1.24			10	0.38	NS
raw		f	0.22	1.28			93	0.04	NS
sm	Mc–Blemish	f1	1.49	3.25			10	0.94	**
raw		f1	1.49	3.25			129	0.57	**

† ln value of the tolerance level.
‡ ln value of the maximum multiplication rate.
§ Probability that $R = 0$.
¶ sm = smoothed data; raw = raw data.

Cumulative negative degree-days (<5 °C) were calculated from monthly average soil temperatures as a measure of the severity of each winter. As another measure of winter severity, cumulative negative degree days below freezing were also calculated. The effect of seasonal soil temperature conditions was determined by regression of the area under the regression line for each relationship against cumulative heat units or cumulative chill units.

RESULTS

Seasonal Multiplication Rates

Across all years, the seasonal multiplication rate of *M. chitwoodi* in potato, barley, alfalfa, and bare-fallow plots was significantly correlated with population levels of the nematode measured the previous fall (Fig. 1a–d; Table 2). For potato, the model explained 65% of the variation in the smoothed dataset and 27% of the variation in the observations on a per-plot basis. The model did not satisfactorily describe the relationship when the nematode population was measured in the spring (Table 2). Due to the difficulties of measuring the population levels in the spring, related to climatic changes and population variability, only the relationships with fall population densities are presented graphically.

Across all years, the seasonal multiplication rate of *P. neglectus* in potato, alfalfa, and barley plots was signifiicantly correlated with population levels of the nematode measured both in the spring and in the previous fall (Fig. 2a–c; Table 2). Seasonal survival rates showed no relationship to either spring or previous fall population levels of *P. neglectus* in plots maintained as bare fallow (Table 2).

Overwinter Survival Rates

Across all years, the overwinter survival rates of *M. chitwoodi* (Fig. 3a; Table 2) and *P. neglectus* (Fig. 3b; Table 2) were strongly correlated with population levels measured in the fall. The model explained 84% of the variability in the smoothed dataset for *M. chitwoodi* and 63% for *P. neglectus.*

Crop Yields in Relation to Nematode Population Densities

Across all years, there was no effect of either spring or previous fall population levels of *M. chitwoodi* on aggregate total potato tuber yields (Fig. 4a; Table 3). Even when examined on an individual-year basis, regression models applied to the datasets did not reveal any relationship between weight of potatoes and numbers of nematodes. On the other hand, composite datasets suggested that lower total potato tuber yields were associated with higher population levels of *P. neglectus* (Fig. 4b; Table 3), with the model explaining 59% of the variability in smoothed potato yield data.

Our data on total potato tuber yield include those tubers classified as Grade no. 1 in various size classes greater than 113.5 g (4 oz), those smaller than 113.5 g (Grade B) and those classified as culls due to blemish. When only Grade no. 1 potato tubers were considered in the analyses,

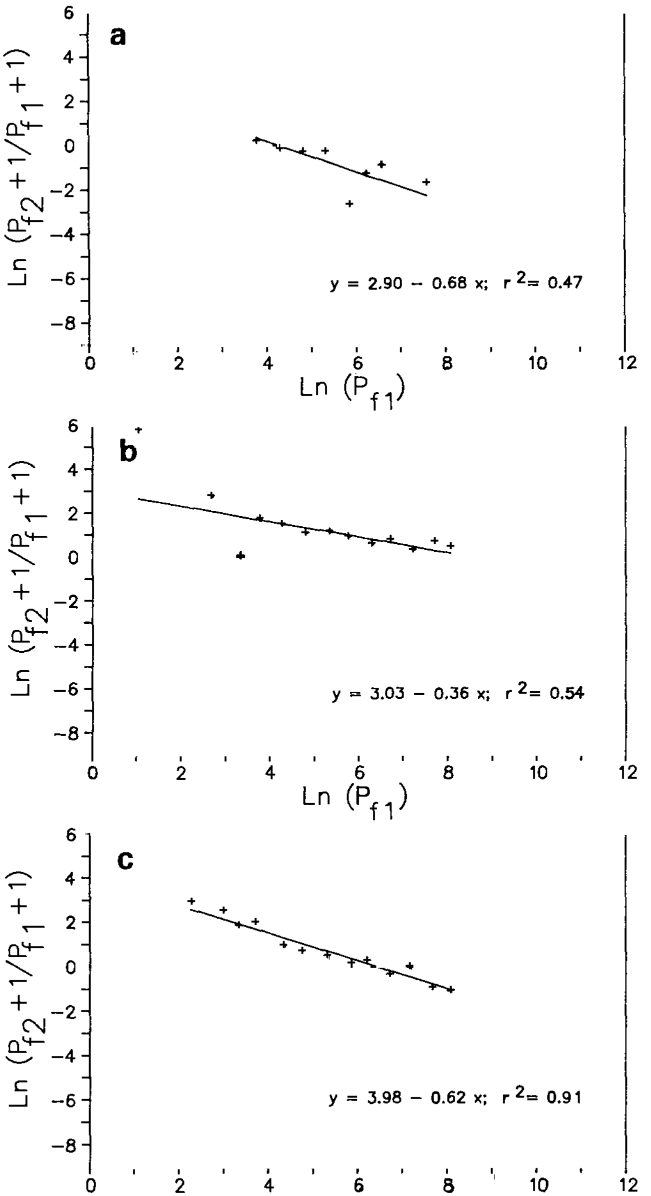

Fig. 2. Seasonal multiplication rates of *Pratylenchus neglectus* in relation to population levels assessed the previous fall: (a) alfalfa; (b) potato; (c) barley.

there was a strong relationship of yield to population levels of *M. chitwoodi* measured the previous fall, but not to population levels of *P. neglectus* (Table 3).

Tuber Blemish Ratings

There was a significant positive correlation between the percentage of tubers with surface blemishes and the population level of *M. chitwoodi* measured either the previous fall or in the spring (Fig. 5a; Table 3). The relationship between potato tuber blemish and population levels of *P. neglectus* measured the previous fall was also positive, but not significant (Fig. 5b; Table 3). There was no relationship of tuber blemish rating to spring population levels of *P. neglectus* (Table 3).

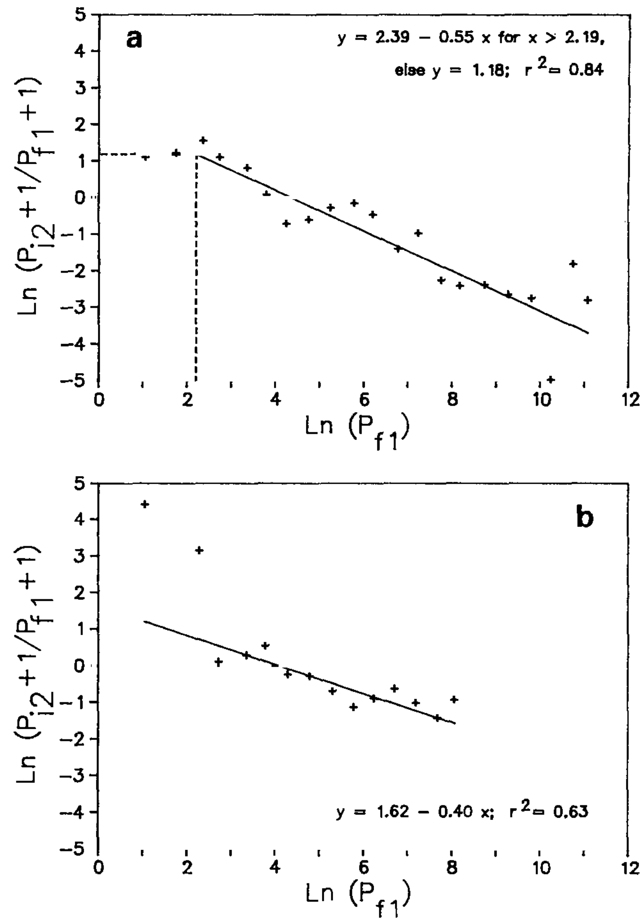

Fig. 3. Overwinter survival of (a) *Meloidogyne chitwoodi* and (b) *Pratylenchus neglectus* in relation to population levels assessed in the fall.

There was a strong relationship between the *M. chitwoodi* population level measured at potato harvest (P_f) and percent tuber surface blemish rating (Fig. 6; Table 3).

Effect of Annual Climatic Variation on Population and Tuber Blemish

There was a linear relationship between the area under the *M. chitwoodi* multiplication rate regression for the nematode population measured in the fall and cumulative summer heat units (DD_5) (Fig. 7a–b). The effect was not apparent for population levels measured in the spring where the relationship of multiplication rate to population level was less robust. There was also a linear relationship between the area under the potato tuber blemish regression line and cumulative summer heat units (Fig. 7c–d). Although straight lines were fitted to the datasets, the arrangements of points were not linear; the areas under the regression lines were relatively stable over a range of thermal

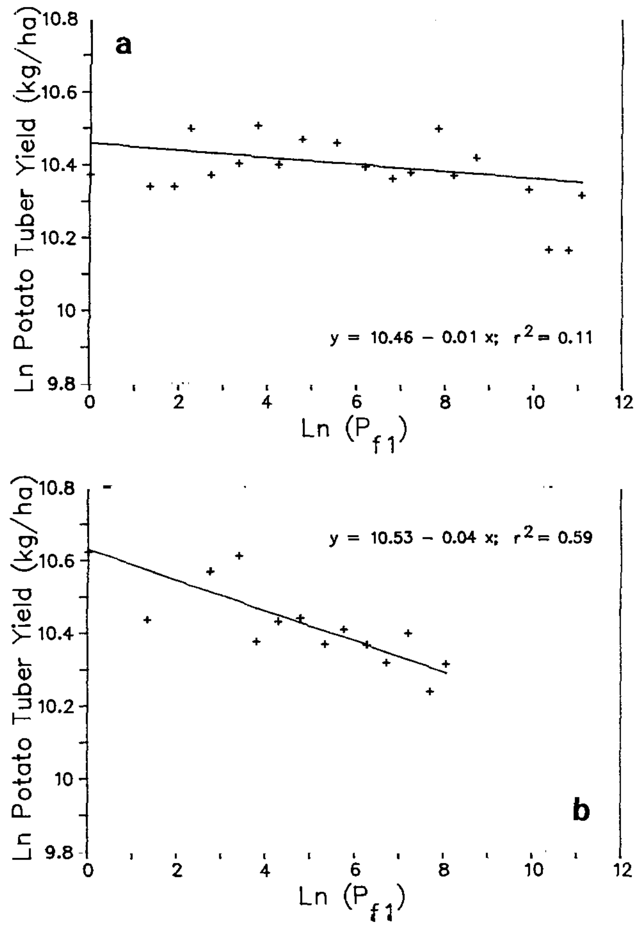

Fig. 4. Total potato tuber yield in relation to population levels of (a) *Meloidogyne chitwoodi* and (b) *Pratylenchus neglectus* assessed the previous fall.

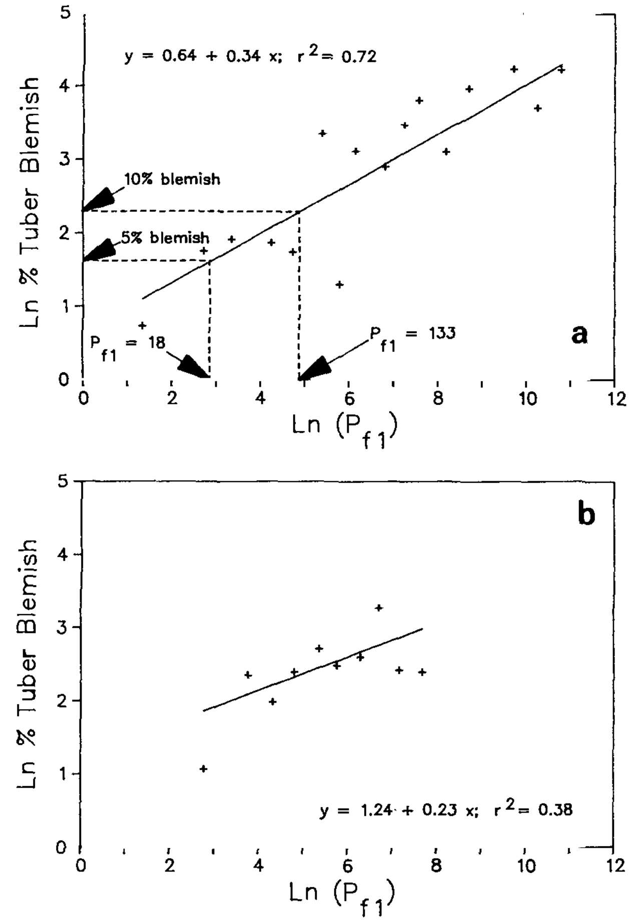

Fig. 5. Potato tuber blemish rating in relation to population levels of (a) *Meloidogyne chitwoodi* and (b) *Pratylenchus neglectus* assessed the previous fall.

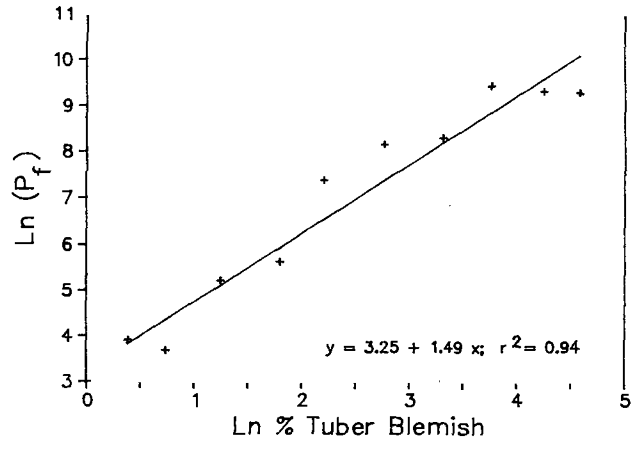

Fig. 6. Relationship of population level of *Meloidogyne chitwoodi* to blemish rating of potato tubers assessed at the same time.

conditions and were considerably greater in one very warm summer (Fig. 7b,d).

There was not a consistent relationship between individual-year overwinter survival and either cumulative chill units below the basal threshold of 5 °C or cumulative subzero temperatures for a given winter.

DISCUSSION

The quantitative relationships resulting from these analyses allow, for advisory purposes and as decision tools for growers, estimation of the following:

1. Expected potato tuber blemish for a population level of *M. chitwoodi* measured either the previous fall or, with lower reliability, in the spring before potato planting.
2. Expected potato yield and quality in relation to population levels of *M. chitwoodi* or *P. neglectus* measured either the previous fall, or in the spring before planting.
3. Expected change in population level (increase or decrease) of *M. chitwoodi* and *P. neglectus* on various crops or under bare-fallow conditions.
4. Expected survival rates of both nematode species over the winter as a function of population levels measured in the fall.
5. Necessary lengths of rotation to nonhost crops to reduce populations of *M. chitwoodi* below levels that

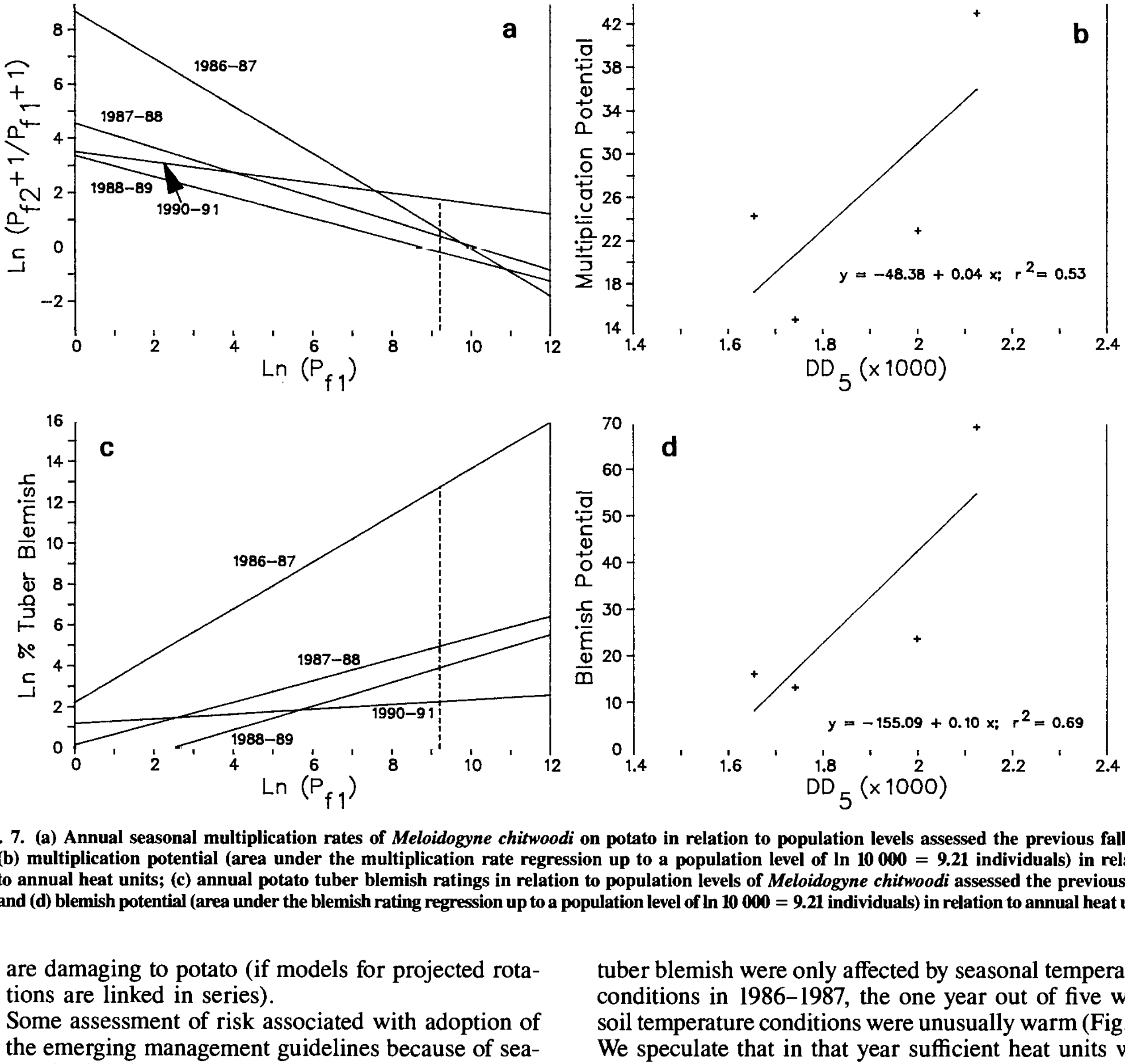

Fig. 7. (a) Annual seasonal multiplication rates of *Meloidogyne chitwoodi* on potato in relation to population levels assessed the previous fall and (b) multiplication potential (area under the multiplication rate regression up to a population level of ln 10 000 = 9.21 individuals) in relation to annual heat units; (c) annual potato tuber blemish ratings in relation to population levels of *Meloidogyne chitwoodi* assessed the previous fall; and (d) blemish potential (area under the blemish rating regression up to a population level of ln 10 000 = 9.21 individuals) in relation to annual heat units.

are damaging to potato (if models for projected rotations are linked in series).

6. Some assessment of risk associated with adoption of the emerging management guidelines because of seasonal climatic variation.

We have used and presented our analyses for relationships derived over several years as an indicator of best mean expectation. Further, we have grouped data according to nematode population density classes to reveal central trends and relationships otherwise masked by sampling error and seasonal and experimental variability. We believe that the central trends provide a rational basis for formulating management decisions, even though actual yields and relationships under future individual-year climatic conditions are unlikely to be precisely predicted by the relationships. We do provide the constants and coefficients for nonsmoothed data (Tables 2 and 3). The associated R^2 values provide indication of the variability in our data, and the range of potential outcomes on an annual basis.

Some of the important relationships for management decisions that emerge from these studies are quite robust. For example, nematode population increase and potato tuber blemish were only affected by seasonal temperature conditions in 1986–1987, the one year out of five when soil temperature conditions were unusually warm (Fig. 6). We speculate that in that year sufficient heat units were accumulated during the potato growing season to allow development of a third generation of *M. chitwoodi*, resulting in greater multiplication and greater potato tuber blemish. As confirming evidence, a strong relationship existed between the *M. chitwoodi* population level measured at potato harvest (P_f) and percent tuber surface blemish rating (Fig. 6). Since this final population level reflects nematode population development, which is related to temperature conditions, we conclude that blemish rating is affected by temperature. Unfortunately, soil temperature data from irrigated crops in the Klamath Basin region are not available for enough years to allow determination of the frequency of occurrence of growing seasons in which >2000 DD$_5$ are accumulated. As such data accrue, the risk of adoption of management decisions based on these data will become more clear. At this time, the best estimate is that the risk of an aberrant year is <20%.

These results confirm earlier studies indicating that there is little impact of population level of *M. chitwoodi* on potato plant growth or total potato tuber yield (e.g., Griffin, 1985; Pinkerton and Santo, 1986). However, there was a strong relationship between yield of Grade no. 1 (marketable) potato tubers and population levels of *M. chitwoodi* the previous fall. That should be an inverse measure of potato tubers not in Grade no. 1, including those culled due to nematode blemish. Nematode management decisions in the potato-based cropping system of the Klamath Basin can be based on the relationship between potato tuber blemish rating and population level of *M. chitwoodi* the previous fall as a primary criterion. At least one composite sample of between 12 and 20 soil cores should be taken for approximately every 2 ha (5 acres) of relatively uniform edaphic conditions (Ferris et al., 1990). The population level of *M. chitwoodi* the previous fall resulting in 10% blemished tubers was 133 eggs and juveniles per liter of soil (Fig. 5a). That population level is measurable, but our ability to detect and assess the population level that would result in 5% potato blemish (18 L^{-1} soil; Fig. 5a) is questionable (Ferris et al., 1990).

It is important that a cropping-system decision made with respect to one nematode species does not exacerbate problems due to another. There was a positive relationship between potato tuber blemish due to *M. chitwoodi* and population levels of *P. neglectus* the previous fall (Fig. 5b). Also, lower potato tuber yields were associated with higher population levels of *P. neglectus* (Fig. 4b). A degree of interference competition between the species was observed in related studies in our laboratory (Umesh and Ferris, 1994, Umesh et al., 1994); consequently, potato damage due to *M. chitwoodi* might be reduced in the field in the presence of *P. neglectus*. The present results appear to be confounded by co-distributed high population levels of both nematodes following suitable host crops, and co-distributed low population levels following host crops less suitable to both species.

Nematicide-based approaches to nematode management in the organic soils of the Klamath basin produce variable results. One distinct advantage of such approaches, however, is that the nematode population is usually reduced to a level below the economic threshold for the planned crop. The effects of rotation programs on nematode populations are less absolute. Management decisions require a greater level of information regarding nematode population levels, expected losses in crop value, and expected quantitative effects of rotation crops on the nematode population. Similar levels and quality of information are required to optimize most other biologically based approaches to nematode management and crop production.

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REFERENCES

Byrd, D.W., Jr., K.R. Barker, H. Ferris, C.J. Nusbaum, W.E. Griffin, R.H. Small, and C.A. Stone. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. J. Nematol. 8:206–212.

Ferris, H. 1984. Nematode damage functions: The problems of experimental and sampling error. J. Nematol. 16:1–9.

Ferris, H. 1985. Density-dependent nematode seasonal multiplication rates and overwinter survivorship: A critical point model. J. Nematol. 17:93–100.

Ferris, H., H. Carlson, D. Viglierchio, B. Westerdahl, F. Wu, C. Anderson, A. Juurma, and D. Kirby. 1993. Host status of selected crops to *Meloidogyne chitwoodi*. Ann. Appl. Nematol. 25:849–857.

Ferris, H., T.A. Mullens, and K.E. Foord. 1990. Stability and characteristics of spatial description parameters for nematode populations. J. Nematol. 22:427–439.

Griffin, G.D. 1985. Host-parasite relationship of *Meloidogyne chitwoodi* on potato. J. Nematol. 17:395–399.

Griffin, G.D. 1991. Differential pathogenicity of four *Pratylenchus neglectus* populations on alfalfa. J. Nematol. 23:380–385.

Griffin, G.D., and K.H. Asay. 1989. Pathological reaction of crested wheatgrass cultivars to four *Meloidogyne chitwoodi* populations. J. Nematol. 21:446–452.

Griffin, G.D., and F.A. Gray. 1990. Biology and pathogenicity of *Pratylenchus neglectus* on alfalfa. J. Nematol. 22:546–551.

Inserra, R.N., G.D. Griffin, and D.V. Sisson. 1983. Effects of temperature and root leachates on embryonic development and hatching of *Meloidogyne chitwoodi* and *M. hapla*. J. Nematol. 15:123–127.

Mojtahedi, H., and G.S. Santo. 1992. *Pratylenchus neglectus* on dryland wheat in Washington. Plant Dis. 76:323.

Mojtahedi, H., G.S. Santo, A.N. Hang, and J.H. Wilson. 1991. Suppression of root-knot nematode populations with selected rapeseed cultivars as green manure. J. Nematol. 23:170–174.

Mojtahedi, H., G.S. Santo, and J.N. Pinkerton. 1988. Differential response of Thor alfalfa to *Meloidogyne chitwoodi* races and *M. hapla*. J. Nematol. 20:410–416.

Nyczepir, A.P., J.H. O'Bannon, G.S. Santo, and A.M. Finley. 1982. Incidence and distinguishing characteristics of *Meloidogyne chitwoodi* and *M. hapla* in potato from the northwestern United States. J. Nematol. 14:347–353.

Pinkerton, J.N., and G.A. McIntyre. 1987. Occurrence of *Meloidogyne chitwoodi* in potato fields in Colorado. Plant Dis. 71:192.

Pinkerton, J.N., and G.S. Santo. 1986. Control of *Meloidogyne chitwoodi* in commercially grown Russet Burbank potatoes. Plant Dis. 70:860–863.

Pinkerton, J.N., G.S. Santo, and H. Mojtahedi. 1986. Population dynamics of *Meloidogyne chitwoodi* in relation to Russet Burbank potato tuber penetration. J. Nematol. 18:627 (abstr.).

Santo, G.S., H. Mojtahedi, and J.H. Wilson. 1988. Host-parasite relationship of carrot cultivars and *Meloidogyne chitwoodi* races and *M. hapla*. J. Nematol. 20:555–564.

Santo, G.S., and J.H. O'Bannon. 1981. Effect of soil temperature on the pathogenicity and reproduction of *Meloidogyne chitwoodi* and *M. hapla* on Russet Burbank potato. J. Nematol. 13:483–486.

Santo, G.S., J.H. O'Bannon, A.M. Finley, and A.M. Golden. 1980. Occurrence and host range of a new root-knot nematode (*Meloidogyne chitwoodi*) in the Pacific Northwest. Plant Dis. 64:951–952.

Santo, G.S., and R.P. Ponti. 1985. Host suitability and reaction of bean and pea cultivars to *Meloidogyne chitwoodi* and *M. hapla*. J. Nematol. 17:77–79.

Siddiqui, I.A., S.A. Sher, and A.M. French. 1973. Distribution of plant parasitic nematodes in California. Calif. Dep. of Food and Agric., Sacramento.

Snedecor, G.W., and W.G. Cochran. 1967. Statistical methods. Iowa State Univ. Press, Ames.

Umesh, K.C., and H. Ferris. 1992. Effects of temperature on *Pratylenchus neglectus* and on its pathogenicity to barley. J. Nematol. 24:504–511.

Umesh, K.C., and H. Ferris. 1994. Influence of temperature and host plant on the interaction between *Pratylenchus neglectus* and *Meloidogyne chitwoodi*. J. Nematol. 26:65–71.

Umesh, K.C., H. Ferris, and D.E. Bayer. 1994. Competition between *Pratylenchus neglectus* and *Meloidogyne chitwoodi*. J. Nematol (in press).

Westerdahl, B.B., H.L. Carlson, J. Grant, J.D. Radewald, N. Welch, C.A. Anderson et al. 1994. Management of plant-parasitic nematodes with a chitin-urea soil amendment and other materials. Ann. Appl. Nematol. 24:669–680.