

Management of Lesion Nematodes and Potato Early Dying with Rotation Crops

J. A. LAMONDIA

Abstract: Soil-incorporated rotation/green manure crops were evaluated for management of potato early dying caused by *Verticillium dahliae* and *Pratylenchus penetrans*. After two years of rotation/green manure and a subsequent potato crop, *P. penetrans* numbers were less after 'Saia' oat/'Polynema' marigold, 'Triple S' sorghum-sudangrass, or 'Garry' oat than 'Superior' potato or 'Humus' rapeseed. The area under the disease progress curve (AUDPC) for early dying was lowest after Saia oat/marigold, and tuber yields were greater than continuous potato after all crops except sorghum-sudangrass. Saia oat/marigold crops resulted in the greatest tuber yields. After one year of rotation/green manure, a marigold crop increased tuber yields and reduced AUDPC and *P. penetrans*. In the second potato crop after a single year of rotation, plots previously planted to marigolds had reduced *P. penetrans* densities and AUDPC and increased tuber yield. Rapeseed supported more *P. penetrans* than potato, but had greater yields. After two years of rotation/green manure crops and a subsequent potato crop, continuous potato had the highest AUDPC and lowest tuber weight. Rotation with Saia oats (2 yr) and *Rudbeckia hirta* (1 yr) reduced *P. penetrans* and increased tuber yields. AUDPC was lowest after *R. hirta*. Two years of sorghum-sudangrass did not affect *P. penetrans*, tuber yield or AUDPC. These results demonstrate that *P. penetrans* may be reduced by one or two years of rotation to non-host or antagonistic plants such as Saia oat, Polynema marigold, or *R. hirta* and that nematode control may reduce the severity of potato early dying.

Key words: *Avena sativa*, *Avena strigosa*, black-eyed Susan, *Brassica napus*, green manure, marigold, management, *Pratylenchus penetrans*, rapeseed, rotation, *Rudbeckia hirta*, *Solanum tuberosum*, *Sorghum bicolor* × *S. sudanense*, sorghum-sudangrass, *Tagetes erecta* × *T. patula*, *Verticillium dahliae*, wilt.

The potato early dying disease results in premature vine senescence and can limit potato (*Solanum tuberosum*) tuber yield by as much as 30 to 50% (Rouse, 1985; Rowe et al., 1985, 1987). Early dying is primarily caused by *Verticillium dahliae*, a fungal vascular wilt pathogen, but co-infection of potato by both *V. dahliae* and the lesion nematode, *Pratylenchus penetrans*, can greatly increase the severity of disease (Martin et al., 1982; Rowe et al., 1987; MacGuidwin and Rouse, 1990).

Disease management has primarily been achieved by soil fumigation with broad-spectrum fungicide/nematicides, but both cost and environmental considerations may limit fumigant use (Rowe et al., 1987). A number of nonchemical controls are being investigated, but each has limitations. *Verticillium*-resistant potato cultivars are under development, but are not yet commercially accepted (Lynch et al., 1997). Management of irrigation and soil nutrient levels may reduce the development of early dying disease in a potato crop, but other cultural practices need to be integrated with these to increase efficacy (Francl et al., 1990; Cappaert et al., 1994). Additional alternative practices include the use of soil amendments. The addition of compost to soil can reduce diseases caused by soilborne fungi (Zhang et al., 1996; Hoitink et al., 1997) and increase water holding and ion exchange capacity of the soil (Maynard, 1994). Maynard (1994) noted that *Verticillium* wilt of eggplant was reduced in compost-amended plots, and LaMondia et al. (1999) concluded that the use of spent mushroom compost increased marketable tuber yield and decreased area under the disease prog-

ress curve (AUDPC) in soils infested with early dying pathogens. The addition of organic matter to potato fields also was associated with reduced populations of *Pratylenchus* spp. (Florini et al., 1987; LaMondia et al., 1999).

The use of rotation crops to manage early dying pathogens has often focused on *Verticillium* (Davis et al., 1996) or on the lesion nematode (Kimpinski et al., 2000; Alexander and Waldenmaier, 2002; Ball-Coelho et al., 2003; Belair et al., 2005), rather than a combination of both pathogens. Rotation crops may be ineffective, even after long-term rotation away from potato (Davis et al., 1994). However, green manures (incorporation of either sudangrass or corn) were found to be more effective in reducing early dying (Davis et al., 1996). While lesion nematodes contribute to the early dying complex, it is uncertain whether nematode control by rotation with nonhost or nematode-antagonistic crops would effectively manage potato early dying.

The objective of our research was to determine the effects of one or two years of rotation/green manure on lesion nematode populations, potato early dying disease, and potato tuber yield.

MATERIALS AND METHODS

Experiment 1: Microplots were established in Windsor, CT, that consisted of plastic waste cans (37.5-cm-diam. top, 30-cm-diam. bottom, 45-cm deep, open at the bottom) buried in soil to within 10 cm of the top and filled with methyl-bromide-fumigated loamy sand field soil (78.0% sand, 16.9% silt, 5.1% clay; 2.8% organic matter; pH 5.6). Soil surrounding the microplots was not fumigated. One hundred and twenty microplots had been previously infested with four pathogen treatments (no pathogens, *Verticillium dahliae* alone, *Pratylenchus penetrans* alone, and both *V. dahliae* and *P. penetrans*)

Received for publication January 27, 2006.

Plant Pathologist/Nematologist, The Connecticut Agricultural Experiment Station Valley Laboratory, P.O. Box 248, Windsor, CT 06095.

The author thanks J. Canepa-Morrison, S. Lamoureux and R. Horvath for technical assistance.

This paper was edited by Stephen Koenning.

and amended or not with spent mushroom compost (2.7 liter/plot, Franklin Mushroom Farms, Franklin, CT) added annually from 1992 to 1995 to the top of appropriate microplots (approximately 2.5 cm in depth = 15 metric tons/ha) and incorporated with a small shovel. By the fall of 1995, microplots containing the four pathogen treatments all contained some level of lesion nematode and *V. dahliae* pathogens (LaMondia et al., 1999). *Pratylenchus* populations ranged from non-detectable to 1,365 individuals/g of rye roots.

Microplots were tilled to turn in the rye cover crop and fertilized with 50 kg N/ha 5–10–10 on 9 May 1996. Plots were blocked by previous treatment (previous pathogen infestation level and compost amendment or no compost amendment), and 24 replicate plots of five crops were planted. Lesion nematode numbers averaged 240.5 and 297.5 in the previously nematode-infested treatments and 5.0 and 56.0 in the two noninfested treatments. *Verticillium* was also present at low levels in the previously noninoculated plots and at high levels in microplots which had been inoculated with the pathogen. A single B-sized tuber of 'Superior' potato was planted in appropriate plots on 9 May 1996, and 'Humus' rapeseed (*Brassica napus*, 10 cm³ seed/plot), 'Saia' oat (*Avena strigosa*, 20 cm³ seed/plot), 'Garry' oat (*Avena sativa*, 20 cm³ seed/plot) and 'Triple S' sorghum-sudangrass (*Sorghum bicolor* × *S. sudanense*, 20 cm³ seeds/plot) were seeded in the other microplots on 15 May 1996. Microplots were side-dressed with 5–10–10 on 11 June 1996 (25 kg N/ha for potato and 12.5 kg N/ha for rotation crops). Plant shoots were cut and tilled into microplot soil by hand on 8 and 9 August 1996 and tilled again on 10 and 11 September 1996. Garry oat was seeded as a cover crop at 50 cm³ seeds/plot on 23 September. Four subsamples of oat were sampled per plot on 15 or 24 October, and 2 g root/microplot were washed free of soil and placed in a flask containing 50 ml water on a wrist-action shaker for 7 d. The oat cover crop was winter-killed due to cold temperatures on 3 November 1996.

Rotation crops were grown again in 1997. Plots were tilled and fertilized as described above on 25 April, and rotation crops seeded on 13 May 1997. The Saia oat treatment was replaced by 'Polynema' marigold (*Tagetes erecta* × *T. patula*, 50 seeds/plot). Microplots were side-dressed as above on 24 June 1997. Plant shoots were cut and tilled as described above on 2 October 1997. No winter cover crop was seeded.

Superior potatoes were grown in all plots in 1998. Certified B-sized seed potatoes were planted 5 to 8 cm below the soil surface in the microplots (1 tuber/microplot), between each microplot within rows, and in border rows (20-cm spacing). Weed control was achieved by the application of Prowl 4E (1.75 liter/ha) Lexone DF (0.74 kg/ha) and Roundup (4.67 liter/ha). Colorado potato beetles and foliar diseases, such as early or late blight, were controlled by applications of

insecticides and fungicides as necessary. Admire 2F was applied to plants at 0.9 liter/ha. Bravo 500 (2.3 liter/ha) and Manzate D (2.2 kg/ha) were rotated. Overhead irrigation (approximately 2.5 cm) was applied when less than 2.5 cm rain fell in the preceding week, and plots were lightly irrigated to cool the plants when air temperatures were greater than 30°C.

Plants were evaluated weekly for up to 8 wk starting with the first symptoms of senescence and continuing until almost all plants had died. The number of live or dead stems and number of compound leaves with or without chlorosis or wilt symptoms were counted weekly for each microplot. The ratio of symptomatic leaves to maximum number of leaves and the ratio of dead stems to total number of stems were integrated over the length of the epidemic and expressed as area-under-the-disease (senescence)-progress-curve (AUDPC) (LaMondia et al., 1999). Plants were not destructively sampled to recover *V. dahliae*, but microsclerotia were associated with senescent stems on early senescing plants. *Verticillium dahliae* was recovered from similar stems after destructive sampling in other experiments (LaMondia et al., 1999).

Plots were harvested after the vines had died. Tubers were dug with a forked spade, graded for size and weighed. Grade A-sized tubers were greater than 5 cm in diameter, grade B-sized tubers were between 3.8 and 5 cm, and culls were less than 3.8 cm in diameter. A- and B-sized tubers constituted marketable yield, and all tubers, regardless of size, were included in total yield. After harvest, plots were seeded with a standard rye cover crop (20 cm³ seeds/plot). Because vines had died over a period of up to 4 wk and nematode recovery efficiencies differ markedly from roots and soil, nematodes were recovered from roots of the rye cover crop to allow consistent comparison between plots. Four subsamples of rye were removed per plot in the fall. Roots were shaken and washed free of soil, and *P. penetrans* was extracted from 2 g root/plot on a rotary arm shaker after 7 d.

Experiment 2: In early May 1999, microplot soil was removed from all microplots in four blocks of 30, and soil within each block was mixed repeatedly to make pathogen densities as uniform as possible. Rotation crops were fertilized and seeded as above on 20 May, after placing the mixed soil into new microplot containers. Rotation crop shoots were cut and incorporated into soil as green manures on 27 August. The effects of a single year of rotation crop on weed ratings were determined on 11 April 2000. A rating of 0 represented no weeds present in plots, and a rating of 10 indicated complete ground cover.

The effects of a single year of a rotation/green manure crop on *P. penetrans*, early dying development, and tuber yields were evaluated by planting 60 microplots to 'Kennebec' potatoes in 2000. The effects of 2 yr of rotation/green manure on *P. penetrans*, early dying devel-

opment, and tuber yields were evaluated in an additional 60 microplots planted for a second year of the same rotation/green manure crop. Black-eyed Susan, *Rudbeckia hirta*, was substituted for the standard oat cultivar (Garry oat) in the second year of the experiment (2000). Plots were fertilized and planted as described above on 1 May 2000.

Weed and insect management of potato plots was achieved as described earlier. Foliar potato pathogens were managed by biweekly application of Acrobat MZ (1.12 kg/ha) fungicide. Potato plots were side-dressed on 29 June as described above. Potato plants were evaluated weekly for 13 wk starting 28 June prior to the first symptoms of senescence and continuing until almost all plants had died. The number of live or dead stems and number of compound leaves with or without chlorosis or wilt symptoms were counted weekly for each microplot. The ratio of symptomatic leaves to maximum number of leaves and the ratio of dead stems to total number of stems were integrated over the length of the epidemic and expressed as AUDPC. Plots were harvested after the vines had died on 25 September 2000, and tuber yield determined as described above. Rye was planted to microplots after the potato harvest was complete. Rotation crops were tilled into soil on 27 September 2000. Nematodes were recovered from roots of 4 subsamples of rye/microplot taken 10 October 2000. Roots were shaken and washed free of soil, and *P. penetrans* was extracted from 2 g root/plot on a rotary arm shaker after 7 d.

All 120 microplots were planted to Kennebec potatoes in 2001. Plots were tilled, fertilized and planted on 13 April and side-dressed on 21 May as described above. Potato plants were evaluated weekly starting on 22 June, prior to the first symptoms of senescence and continuing for 11 wk until almost all plants had died. Tubers were harvested on 19 September, and 'Porter' oats planted as a winter cover. Four subsamples of oat plants per microplot were taken on 3 and 10 October 2001. Roots were shaken and washed free of soil, and *P. penetrans* was extracted from 2 g root/plot on a rotary arm shaker after 7 d.

Data were analyzed by Analysis of Variance and means separated by Fisher's Least Significant Difference Test.

RESULTS

Experiment 1: After two years of rotation and green manure crops and a subsequent potato crop, *P. penetrans* populations extracted from cover crop roots following the potato crop were less ($P = 0.001$) for microplots which had been planted to Saia oat/Polynema marigold or Triple S sorghum-sudangrass, than in microplots planted to Superior potato or Humus rapeseed (Table 1). Lesion nematode numbers were greater ($P = 0.001$) in plots that had been previously amended with

TABLE 1. The effect of rotation crops in 1996 and 1997 and compost amendment on lesion nematode densities from rye cover crop roots and potato early dying development, 1998.

1996 Rotation crop	1997 Rotation crop	<i>Pratylenchus</i> /2 g root	AUDPC ^a
Superior potato	Superior potato	219 bc ^b	14.7 b
Humus rapeseed	Humus rapeseed	376 c	14.0 b
Saia oat	Polynema marigold	3 a	9.9 a
Triple S sorghum-sudangrass	Triple S	8 a	12.8 a
Garry oat	Garry oat	124 ab	14.7 b
$P =$		0.001	0.0001
Compost		296	12.8
No compost		71	13.3
$P =$		0.001	ns

^a Area under the Disease Progress Curve.

^b Means within columns followed by the same letter are not different (ANOVA and Fishers LSD, $P = 0.05$).

spent mushroom compost. The AUDPC was reduced ($P = 0.0001$) after Saia oat/Polynema marigold, compared with all other treatments. The previous application of spent mushroom compost had no effect on the AUDPC.

Total, marketable, and A-sized tuber yields were greater ($P = 0.01$) than continuous potato after all rotation crops except Triple S sorghum-sudangrass (Table 2). Saia oat/Polynema marigold rotation crops resulted in the greatest tuber yields and were more than all other rotation/green manure crops except Humus rapeseed ($P = 0.05$). Microplots previously amended with spent mushroom compost had greater tuber yields than nonamended microplots ($P = 0.002$). Humus rapeseed was a host of the lesion nematode, had no effect on AUDPC, and had increased yields compared with potato, but not the standard oat rotation crop.

Experiment 2: After a single year of rotation/green manure, a Polynema marigold rotation crop resulted in lower *P. penetrans* numbers in roots of rye grown after the potato crop than continuous potato, had greater

TABLE 2. The effect of rotation crops in 1996 and 1997 and compost amendment on potato tuber yield in microplots, 1998.

Rotation crops	Grade 'A' and 'B' ^a	Tuber wt (g)	
		Grade 'A' wt	Total
Superior potato	763 c ^b	273 d	851 c
Humus rapeseed	984 ab	569 b	1,030 ab
Saia oat/Polynema marigold	1,076 a	733 a	1,138 a
Triple S sorghum-sudangrass	867 bc	387 cd	906 bc
Garry oat	932 b	511 bc	987 b
$P =$	0.009	0.0001	0.01
Compost	1,034	658	1,082
No compost	875	421	938
$P =$	0.001	0.0001	0.002

^a Marketable tuber weight.

^b Means within columns followed by the same letter are not different (ANOVA and Fishers LSD, $P = 0.05$).

marketable tuber yields than potato and all other crops, and reduced AUDPC for early dying symptoms over the season compared with continuous potato or all other crops ($P = 0.05$) (Table 3). Humus rapeseed had higher *P. penetrans* densities than all other plants and early senescence as measured by AUDPC. Marketable tuber yields were similar for all crops except marigold.

In the second potato crop grown after a single year of rotation, *P. penetrans* populations remained less than continuous potato ($P = 0.05$), AUDPC was lower, and tuber yields were higher after *Polynema marigold*. Rapeseed, which maintained higher lesion nematode numbers than potato or the standard oat rotation crop, resulted in higher tuber yields than either continuous potato or the standard oat rotation crop (Table 4). Humus rapeseed had the highest *P. penetrans* densities of all crops grown, similar AUDPC values to all crops except marigold, yet had higher tuber yields than either continuous potato or the standard oat rotation crop.

Weed growth ratings (on a scale of 0–10) were suppressed by rotation/green manure crops compared to potato ($P = 0.001$). Sorghum-sudangrass (rating of 1.5) and rapeseed (1.7) reduced weed ratings more than the other rotation crops (2.4 to 2.8) or potato (3.9) ($P = 0.05$). The predominant weeds present were winter annuals such as whitlowwort, *Draba verna*, and common chickweed, *Stellaria media* (data not shown).

After two years of rotation and green manure crops and a subsequent potato crop, AUDPC was highest and marketable tuber weight lowest for continuous potato. Lesion nematode densities were low after two years of Saia oat, *Polynema marigold* or after *R. hirta* growth (after oat) in the second year (Table 5). Rotation with Saia oat (two years) and *R. hirta* (one year) reduced lesion nematode numbers and increased tuber yields. The AUDPC was lower after *R. hirta* than for any other treatment. Two years of sorghum-sudangrass did not have significant impacts on *P. penetrans* populations, tuber yield or AUDPC. Humus rapeseed had higher lesion nematode densities than all other crops, similar

TABLE 3. The effect of a single year of rotation/green manure in 1999 on *Pratylenchus* populations, tuber yield, and potato early dying development in microplots, 2000.

Rotation crops	<i>Pratylenchus</i>	'A' and 'B' tuber wt ^a	AUDPC ^b
Superior potato	554 b ^c	782.0 b	26.2 bc
Humus rapeseed	1,160 c	858.8 b	28.8 d
Saia oat	430 b	809.7 b	27.8 cd
<i>Polynema marigold</i>	23 a	1,224.5 a	21.1 a
Triple S sorghum-sudangrass	206 ab	826.7 b	24.3 b
Garry oat	307 ab	760.9 b	26.8 cd
<i>P</i> =	0.001	0.005	0.0001

^a Marketable tuber weight.

^b Area under the Disease Progress Curve.

^c Means within columns followed by the same letter are not different (ANOVA and Fishers LSD, $P = 0.05$).

TABLE 4. The effect of a single year of rotation/green manure crops in 1999 on a second year of potato tuber yield, potato early dying development, and lesion nematodes in microplots, 2001.

1999 Rotation crop	2000 Crop	'A' and 'B' tuber wt ^a	AUDPC ^b	<i>Pratylenchus</i>
Superior potato	Potato	787.7 c ^c	35.9 bc	665 b
Humus rapeseed	Potato	945.1 ab	36.6 bc	1,279 c
Saia oat	Potato	793.8 c	38.1 c	259 ab
<i>Polynema marigold</i>	Potato	1,051.7 a	32.5 a	150 a
Triple S sorghum-sudangrass	Potato	887.0 bc	35.1 ab	259 ab
Garry oat	Potato	799.5 c	37.5 bc	508 ab
<i>P</i> =		0.0001	0.001	0.001

^a Marketable tuber weight.

^b Area under the Disease Progress Curve.

^c Means within columns followed by the same letter are not different (ANOVA and Fishers LSD, $P = 0.05$).

AUDPC values to all crops except continuous potato, yet still had high marketable tuber weights similar to *Polynema marigold* and oat followed by *R. hirta*.

DISCUSSION

Soil-incorporated rotation/green manure crops, such as sudangrass, have previously been demonstrated to reduce potato early dying disease more than fallow or rotation crop growth without incorporation (Davis et al., 1996; Kratochvil et al., 2004). The effects of a green manure on early dying were attributed to both reduced *V. dahliae* inoculum in soil and also to other undetermined factors (Davis et al., 1996). Sudangrass and sorghum-sudangrass hybrids have been shown to reduce root-knot (Viaene and Abawi, 1998) and lesion nematode populations in soil (Thies et al., 1995; LaMondia et al., 2002; Kratochvil et al., 2004). One possibility for the reduction in potato early dying without reduced *V. dahliae* propagules might be an impact on lesion nematode populations contributing to the disease complex. Other possibilities include the indirect effects of rotation/green manure crops on the physical effects of soil structure and nutrient availability (Davis et al., 1996)

TABLE 5. The effect of rotation/green manure crops in 1999 and 2000 on potato tuber yield, potato early dying development, and lesion nematodes in microplots, 2001.

1999 Rotation crop	2000 Crop	'A' and 'B' tuber wt ^a	AUDPC ^b	<i>Pratylenchus</i>
Superior potato	Potato	550.5 d ^c	39.2 c	1,135 b
Humus rapeseed	Humus	950.2 a	35.3 ab	2,165 c
Saia oat	Saia	773.2 bc	36.8 bc	205 a
<i>Polynema marigold</i>	<i>Polynema</i>	887.7 ab	35.9 b	30 a
Triple S sorghum-sudangrass	Triple S	726.4 c	36.8 bc	598 ab
Garry oat	<i>R. hirta</i>	934.9 ab	33.2 a	184 a
<i>P</i> =		0.0001	0.001	0.001

^a Marketable tuber weight.

^b Area under the Disease Progress Curve.

^c Means within columns followed by the same letter are not different (ANOVA and Fishers LSD, $P = 0.05$).

and the indirect effects on soil microbes, some of which may be antagonistic to soilborne pathogens (Wiggins and Kinkel, 2005). Annual application of spent mushroom compost increased potato growth and yield, delayed senescence and reduced lesion nematode densities after potato (LaMondia et al., 1999). In the present study, microplots which had previously received compost had increased tuber yield, but no reduction in AUDPC. Lesion nematode densities were higher after potatoes grown in plots which had previously received compost application (one to five years before), in direct contrast to the reduced nematode densities observed after annual application of spent mushroom compost prior to planting tubers (LaMondia et al., 1999). Spent mushroom compost may influence potato nutrition or physiology, the physical properties of soil, pathogen populations, microbial ecology in soil, antibiosis, and possible systemic-acquired-resistance in relation to potato early dying (LaMondia et al., 1999). The mechanism(s) of the previously observed suppression appears to be associated with the annual application of fresh spent mushroom compost.

Our results have demonstrated that *P. penetrans* densities may be reduced by one or two years of rotation to nonhost or antagonistic plants such as Saia oat, *Polynema marigold*, or *R. hirta*. Saia oat has been shown to control lesion nematodes (Townshend, 1989; Vrain et al., 1996; LaMondia et al., 2002). *Polynema marigold* has nematicidal activity against root-knot (Ploeg, 2002) and root lesion nematodes (Riga et al., 2005). *Rudbeckia hirta* reduced root-knot nematode populations (LaMondia, 1997) and lesion nematode densities in pots (Potter and McKeown, 2002) and in vitro due to root exudation of nematicidal thiarubrine C (de Viala et al., 1998). *Polynema marigold* and *R. hirta* had the most significant impacts on lesion nematode densities. A single year of rotation to these plants was sufficient to reduce nematode densities, delay potato senescence (reduce AUDPC) and increase tuber yields. However, the effects of rotation/green manure crops on *V. dahliae* were not directly determined in these experiments. Soil dilution plating can be quite variable and may not correlate well with disease development (Ter-morshuizen et al., 1998). Rather, the ratio of symptomatic leaves to maximum number of leaves was integrated over the length of the epidemic and expressed as AUDPC. The direct effects of these plants on *V. dahliae* propagules will need to be determined to evaluate whether the impact on potato early dying is primarily through the fungal or nematode component of the disease complex, or by some other means.

Simply reducing lesion nematode populations in microplots did not always result in reduced early dying disease (expressed as AUDPC) and increased tuber yields in these experiments. For example, two years of sorghum-sudangrass resulted in low *P. penetrans* populations, but AUDPC was not different from potato, and

tuber yields were not increased relative to continuous potato. On the other hand, Humus rapeseed maintained the highest levels of lesion nematodes throughout the course of the experiments, greater than potato, but still resulted in increased tuber yields. The AUDPC values following Humus rotation were similar to continuous potato or oat rotation crops, suggesting that *V. dahliae* was involved in potato early dying senescence.

Brassica spp., including rapeseed, have been investigated as a biofumigant crop for managing plant-pathogenic nematodes and fungi with isothiocyanates, volatiles and other chemicals (Olivier et al., 1999; Zasada and Ferris, 2004; Matthiessen and Kirkegaard, 2006). *Brassicacae* have been inconsistent in efficacy, perhaps for several reasons. Rapeseed has been reported as a host (Mojtahedi et al., 1991) or a poor host of *M. chitwoodi* (Al-Rehiyani and Hafez, 1998), but green manure incorporation of shoots reduced densities of *M. chitwoodi* but not *P. neglectus* and increased marketable potato yields. *Brassicacae* reduced *P. neglectus* densities (Potter et al., 1998), but different cultivars with different glucosinolate profiles may affect different nematodes or additional *Pratylenchus* spp. differently (Webb, 1996; Zasada and Ferris, 2004). *Brassica juncea* but not *B. napus* reduced *Xiphinema index* densities as green manures (Aballay et al., 2004). *Brassica* spp. and cultivars also likely differ in efficacy against *V. dahliae* (Olivier et al., 1999). Wiggins and Kinkel (2005) reported that canola green manure did not reduce *Verticillium* wilt of potato compared to fallow.

Our results differ from Davis et al. (1996) in that sorghum-sudangrass did not control potato early dying. The lack of control in our experiments may be explained by sudangrass vs. sorghum-sudangrass differences, differences in cultivars, location effects, or differences in soil microbial ecology that may affect plant breakdown products or soil nutrient levels. A lack of yield response may also be due to the slow breakdown of woody stalks and effects on available nitrogen or the buildup of plant breakdown products that may reduce plant growth response (Ball-Coelho et al., 2001). The incorporation of sorghum-sudangrass residues suppressed winter annual weed growth in Experiment 2, and potato growth may also have been affected by these residues.

The increased tuber yields that were observed in these experiments after growth and green manure incorporation of rotation crops such as *Polynema marigold* and *Rudbeckia hirta*, or rapeseed in the absence of nematode control or reduction in the AUDPC, may be due to indirect effects rather than direct effects on pathogen densities in soil. Green manure treatments may contribute to disease management by changing the *Streptomyces* communities in soils, leading to pathogen suppression (Wiggins and Kinkel, 2005) or resulting in bacterial communities that may induce plant systemic resistance (Cohen et al., 2005).

While these results demonstrate the potential for rotation/green manure crops to manage lesion nematodes, reduce the expression of potato early dying as measured by AUDPC, and increase tuber yields, they are not immediately practical. Saia oat is not commercially available. In addition, although *Polynema marigold* and *R. hirta* seeds are commercially available, neither plant has commercial value beyond its use as a rotation/green manure crop. Both plants are difficult to establish and do not compete well with weeds. Additional research will be necessary either to aid in the establishment of these plants or identify additional plants better able to manage practically potato early dying.

LITERATURE CITED

- Aballay, E. Sepulveda, R., and Insunza, V. 2004. Evaluation of five nematode-antagonistic plants used as green manure to control *Xiphinema index* Thorne et Allen on *Vitis vinifera* L. *Nematropica* 34:45–51.
- Alexander, S. A., and Waldermaier, C. M. 2002. Suppression of *Pratylenchus penetrans* populations in potato and tomato using African marigolds. *Journal of Nematology* 34:130–134.
- Al-Rehiyani, S., and Hafez, S. 1998. Host status and green manure effect of selected crops on *Meloidogyne chitwoodi* race 2 and *Pratylenchus neglectus*. *Nematropica* 28:213–230.
- Ball-Coelho, B. R., Bruin, A. J., Roy, R. C., and Riga, E. 2003. Forage pearl millet and marigold as rotation crops for biological control of root-lesion nematodes in potato. *Agronomy Journal* 95:282–292.
- Ball-Coelho, B. R., Reynolds, L. B., Back, A. J., and Potter, J. W. 2001. Residue decomposition and soil nitrogen are affected by mowing and fertilization of marigold. *Agronomy Journal* 93:207–215.
- Belair, G., Dauphinais, N., Fournier, Y., Dangi, O. P., and Clement, M. F. 2005. Effect of forage and grain pearl millet on *Pratylenchus penetrans* and potato yields in Quebec. *Journal of Nematology* 37:78–82.
- Cappaert, M. R., Powelson, M. L., Christensen, N. W., Stevenson, W. R., and Rouse, D. I. 1994. Assessment of irrigation as a method of managing potato early dying. *Phytopathology* 84:792–800.
- Cohen, M. F., Yamasaki, H., and Mazzola, M. 2005. *Brassica napus* seed meal soil amendment modifies microbial community structure, oxide production and incidence of *Rhizoctonia* root rot. *Soil Biology and Biochemistry* 37:1215–1227.
- Davis, J. R., Huisman, O. C., Westermann, D. T., Hafez, S. L., Everson, D. O., Sorensen, L. H., and Schneider, A. T. 1996. Effects of green manures on Verticillium wilt of potato. *Phytopathology* 86:444–453.
- Davis, J. R., Huisman, O. C., Westermann, D. T., Sorensen, L. H., Schneider, A. T., and Stark, J. C. 1994. The influence of cover crops on the suppression of Verticillium wilt in potato. Pp. 332–341 in G. W. Zehnder, M. L. Powelson, R. K. Jannson, and K. V. Ramay, eds. *Advances in Potato Pest Biology and Management*. St. Paul, MN: The American Phytopathological Society.
- de Viala, S. S., Brodie, B. B., Rodríguez, E., and Gibson, D. M. 1998. The potential of thiarubrine C as a nematocidal agent against plant-parasitic nematodes. *Journal of Nematology* 30:192–200.
- Florini, D. A., Loria, R., and Kotcon, J. B. 1987. Influence of edaphic factors and previous crops on *Pratylenchus* spp. population densities in potato. *Journal of Nematology* 19:85–92.
- Francl, L. J., Madden, L. V., Rowe, R. C., and Riedel, R. M. 1990. Correlation of growing season environmental variables and the effect of early dying on potato yield. *Phytopathology* 80:425–432.
- Hoitink, H. A. J., Stone, A. G., and Han, D. Y. 1997. Suppression of plant diseases by composts. *HortScience* 32:184–187.
- Kimpinski, J., Arsenault, W. J., Gallant, C. E., and Sanderson, J. B. 2000. The effect of marigolds (*Tagetes* spp.) and other cover crops on *Pratylenchus penetrans* and on following potato crops. Supplement to the *Journal of Nematology* 32:531–536.
- Kratovich, R. J., Sardaneli, S., Everts, K., and Gallagher, E. 2004. Evaluation of crop rotation and other cultural practices for management of root-knot and lesion nematodes. *Agronomy Journal* 96:1419–1428.
- LaMondia, J. A. 1997. Management of *Meloidogyne hapla* in herbaceous perennial ornamentals by sanitation and resistance. *Journal of Nematology* 29:717–720.
- LaMondia, J. A., Elmer, W. H., Mervosh, T. L., and Cowles, R. S. 2002. Integrated management of strawberry pests by intercropping. *Crop Protection* 21:837–846.
- LaMondia, J. A., Gent, M. P. N., Ferrandino, F. J., Elmer, W. H., and Stoner, K. A. 1999. The effect of compost amendment or straw mulch on potato early dying disease development and yield. *Plant Disease* 83:361–366.
- Lynch, D. R., Kawchuk, L. M., Hachey, J., Bains, P. S., and Howard, R. J. 1997. Identification of a gene conferring high levels of resistance to Verticillium wilt in *Solanum chacoense*. *Plant Disease* 81:1011–1014.
- MacGuidwin, A. E., and Rouse, D. I. 1990. Role of *Pratylenchus penetrans* in the potato early dying disease of Russet Burbank potato. *Phytopathology* 80:1077–1082.
- Martin, M. J., Riedel, R. M., and Rowe, R. C. 1982. *Verticillium dahliae* and *Pratylenchus penetrans*: Interactions in the early dying complex of potato in Ohio. *Phytopathology* 72:640–644.
- Matthiessen, J. N., and Kirkegaard, J. A. 2006. Biofumigation and enhanced biodegradation: Opportunity and challenge in soilborne pest and disease management. *Critical Reviews in Plant Sciences* 25:235–265.
- Maynard, A. A. 1994. Sustained vegetable production for three years using composted animal manures. *Compost Science Utilization* 2:88–96.
- Mojtahedi, H., Santo, G. S., Hang, A. N., and Wilson, J. H. 1991. Suppression of root-knot nematode populations with selected rape-seed cultivars as green manure. *Journal of Nematology* 23:170–174.
- Olivier, C., Vaughn, S. F., Mizubuti, E. S. G., and Loria, R. 1999. Variation in allyl isothiocyanate production within *Brassica* species and correlation with fungicidal activity. *Journal of Chemical Ecology* 25:2687–2701.
- Ploeg, A. T. 2002. Effects of selected marigold varieties on root-knot nematodes and tomato and melon yields. *Plant Disease* 86:505–508.
- Potter, J. W., and McKeown, A. W. 2002. Inhibition of *Pratylenchus penetrans* by intercropping of *Rudbeckia hirta* and *Lycopersicon esculentum* in pot cultivation. *Phytoprotection* 83:115–120.
- Potter, M. J., Davies, K., and Rathjen, A. J. 1998. Suppressive impact of glucosinolates in *Brassica* vegetative tissues on root lesion nematode *Pratylenchus neglectus*. *Journal of Chemical Ecology* 24:67–80.
- Riga, E., Hooper, C., and Potter, J. 2005. In vitro effect of marigold seed exudates on plant parasitic nematodes. *Phytoprotection* 86:31–35.
- Rouse, D. I. 1985. Some approaches to prediction of potato early dying disease severity. *American Potato Journal* 62:187–193.
- Rowe, R. C., Davis, J. R., Powelson, M. L., and Rouse, D. I. 1987. Potato early dying: Causal agents and management strategies. *Plant Disease* 71:482–489.
- Rowe, R. C., Riedel, R. M., and Martin, M. J. 1985. Synergistic interactions between *Verticillium dahliae* and *Pratylenchus penetrans* in potato early dying disease. *Phytopathology* 75:412–418.
- Termorshuizen, A. J., Davis, J. R., Gort, G., Harris, D. C., Huisman, O. C., Lazarovits, G., Locke, T., Vara, J. M. M., Mol, L., Paplomatas, E. J., Platt, H. W., Powelson, M., Rouse, D. I., Rowe, R. C., and Tsrer, L. 1998. Interlaboratory comparison of methods to quantify microsclerotia of *Verticillium dahliae* in soil. *Applied and Environmental Microbiology* 64:3846–3853.
- Thies, J. A., Petersen, A. D., and Barnes, D. K. 1995. Host suitability of forage grasses and legumes for root-lesion nematode *Pratylenchus penetrans*. *Crop Science* 35:1647–1651.
- Townshend, J. L. 1989. Population densities of four species of root-lesion nematodes (*Pratylenchus*) in the oat cultivars, Saia and OAC Woodstock. *Canadian Journal of Plant Science* 69:903–905.

Viaene, N. M., and Abawi, G. S. 1998. Management of *Meloidogyne hapla* on lettuce in organic soil with sudangrass as a cover crop. *Plant Disease* 82:945–952.

Vrain, T., DeYoung, R., Hall, J., and Freyman, S. 1996. Cover crops resistant to root-lesion nematodes in raspberry. *HortScience* 31:1195–1198.

Webb, R. M. 1996. In vitro studies of six species of *Pratylenchus* (Nematoda:Pratylenchidae) on four cultivars of oilseed rape (*Brassica napus* var *oleifera*). *Nematologica* 42:89–95.

Wiggins, B. E., and Kinkel, L. L. 2005. Green manures and crop sequences influence potato diseases and pathogen inhibitory activity of indigenous *Streptomyces*. *Phytopathology* 95:178–185.

Zasada, I. A., and Ferris, H. 2004. Nematode suppression with brassicaceous amendments: Application based upon glucosinolate profiles. *Soil Biology and Biochemistry* 36:1017–1024.

Zhang, W., Dick, W. A., and Hoitink, H. A. 1996. Compost-induced systemic acquired resistance in cucumber to *Pythium* root rot and anthracnose. *Phytopathology* 86:1066–1070.