Supplement to the Journal of Nematology 27(4S):654–660. 1995.

Impact of Multi-year Cropping Regimes on *Solanum tuberosum* Tuber Yields in the Presence of *Pratylenchus penetrans* and *Verticillium dahliae*

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Abstract: Five cropping regimes involving combinations of 2 legumes, alfalfa (*Medicago sativa*) and yellow sweet clover (*Melilotus officinalis*), 2 monocots, corn (*Zea mays*) and sudax (*Sorghum halupeuse* × *Sorghum sudanese*), and potato (*Solanum tuberosum* cv. Superior) were tested for their impact on potato yields in a field infested with *Pratylenchus penetrans* and *Verticillium dahliae*. No differences in 1990 tuber yields were observed among the five cropping regimes ($P < 0.05$). In 1991, yields following 1 year of corn, sudax, sweet clover, or alfalfa and 2 years of potato were not different from that of 3 years of continuous potato ($P < 0.05$). Two years of sweet clover or alfalfa followed by potato resulted in significantly increased potato tuber yields compared with 3 years of potato ($P < 0.05$). The 2-year legume and 2-year grain rotations resulted in lower *P. penetrans* population densities at the end of the 3-year rotation compared with 3 years of continuous potato ($P < 0.01$). The highest preplant *V. dahliae* population density (34 cfu/g soil), together with a *P. penetrans* density of 12/100 cm^3 of soil was in the sudax-sudax-potato cropping regime and resulted in the lowest potato tuber yield. The highest preplant *P. penetrans* population density (54/100 cm^3 soil), together with a *V. dahliae* population density of 19.5 cfu/g soil was observed in the corn-corn-potato cropping regime and resulted in the second lowest potato tuber yield in 1991. After 3 years, potato tuber yields were negatively related to preplant densities of *V. dahliae* ($r^2 = 0.237$), *P. penetrans* ($r^2 = 0.175$), and both pathogens ($r^2 = 0.380$). A comprehensive regression model was developed to isolate pathogen effects on potato yields from cropping regime effects encompassing all 10 cropping regimes ($r^2 = 0.915$).

Key words: cropping regime, interaction, nematode, potato tuber yield, *Pratylenchus penetrans*, lesion nematode, *Solanum tuberosum*, *Verticillium dahliae*, verticillium wilt.

Premature vine death and declining tuber yields limit potato (*Solanum tuberosum*) production in Michigan, Wisconsin, Ohio, Idaho, and the Red River Valley (23). Potato early dying disease frequently involves 2 major soilborne pathogens, *Verticillium dahliae* and *Pratylenchus penetrans* (2,4,10, 12,13,17,18,20,24) (R. Chase, Pers. Comm).

Crop rotation has long been considered an important part of disease management schemes for potato early dying (2,3,23). Five- to 10-year rotations with grains can effectively decrease *V. dahliae* in soil (5). Short-term crop rotations have been evaluated in potato production in the presence of *P. penetrans* and *V. dahliae* (2,23). Easton et al. (6) reported on a 2-year potato rotation with *V. dahliae*-immune hosts. In addition, rotation of potato with grains is a common practice in some locations for Colorado potato beetle control (8). Our objective was to evaluate the impact of 3-year cropping regimes on *S. tuberosum* tuber yields in a field infested with *P. penetrans* and *V. dahliae*.

MATERIALS AND METHODS

Experimental design: A 3-year crop rotation experiment was initiated in 1989 at the Michigan State University Potato Research Farm at Entrican, MI (Montcalm County). A high incidence of potato early dying was observed at this site during the previous 15 years. The research site was separated from others by a 9-m cultivated alley. Each 4-row plot was 15-m in length. The experiment was conducted in randomized complete blocks with five replications of 10 treatments.

The cropping regimes in 1989 and 1990 included 1 and 2 years of alfalfa (*Medicago*

Received for publication 20 April 1995.
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We thank John Davenport for technical assistance and field work. We thank H. Melakeberhan and M. F. Berney for reviewing. Funded by USDA Cooperative State Research Service, Michigan Potato Research Special Grant.

sativa cv. Vernal), yellow sweet clover (*Melilotus officinalis* cv. Mannoth), corn (*Zea mays,* St. Joseph Valley 758-B-25), and sudax (*Sorghum halupeuse* × *Sorghum sudanese*). Rye (*Secale cereale* cv. Wheeler) was included in 1990, and 3 years of consecutive potato (*S. tuberosum* cv. Superior) production was used as a control for rotation effects. Designations of potato-potato-potato (P-P-P), potato-rye-potato (P-R-P), corn-potato-potato (C-P-P), corn-corn-potato (C-C-P), sudax-potato-potato (S-P-P), sudax-sudax-potato (S-S-P), clover-potato-potato (Cl-P-P), clover-clover-potato (Cl-Cl-P), alfalfa-potato-potato (A-P-P), and alfalfa-alfalfa-potato (A-A-P) represent the crops grown in 1989, 1990, and 1991, respectively.

Cultural practices: The research site was a Montcalm loamy sand soil (75.3% sand, 13.7% silt, 11% clay; 1.1% organic matter; pH 6.7), maintained under a solid set overhead irrigation system. After the 1989 and 1990 harvests, plant residues were left in the field and incorporated into the soil the following spring. The research site was managed according to conventional recommendations for commercial potato production in Michigan (R. Chase, pers. comm.). Pathogen-free potato seed pieces (50–57 g), obtained from Carl Hessler and Sons Potato Farm, Rockford, MI, were machine-planted ca. 10 cm deep and 21 cm apart on 21 May 1991 with 0.86 m between rows.

Soilborne pathogen assays: Soil samples were taken to assess *V. dahliae* and *P. penetrans* population densities at the beginning of the season. *Pratylenchus penetrans* population densities were also determined at mid-season (38 days after planting in 1991), and at the end of the growing season. Eight to 12 soil cores were collected in the planted row of the center 2 rows of each plot with a modified 600 cm^3 United States Department of Agriculture, Division of Plant Industry field subsampling tool (7), and combined with thorough mixing. Root samples were collected during the midseason sampling with a shovel. Both soil and root samples were placed in plastic bags and stored at 4 C in a cooler.

One subsample (25–75 g soil) was air-dried at 20–24 C for at least 4 weeks, and processed for *V. dahliae* by dilution plating (19). Four replicate 1-ml aliquots of soil suspension were plated on the medium and incubated at 22–24 C in the dark for 2 weeks. *Verticillium dahliae* colony-forming units (cfu) per plate were counted under ×40 magnification, and expressed as cfu per g soil.

A 100-cm^3 subsample of soil was processed for *P. penetrans* by a modified centrifugal flotation technique (11). Root samples were processed within 24 hours after collection. The roots were rinsed and a 1-g subsample was arbitrarily selected and cut into pieces ca. 2 cm long. The tissue was incubated in a solution of ethoxyethyl mercuric chloride (10 ppm) and dihydrostreptomycin sulfate (50 ppm) on a gyratory shaker at 100 rpm for 48 hours. Vermiform stages of *P. penetrans* retained on a 38-μm-pore sieve were rinsed, counted, and expressed as numbers per 100 cm^3 soil, or numbers per g root tissue.

Identification of *V. dahliae* and separation from similar fungi was as described by Mace et al. (14). The dominant *Pratylenchus* species was identified as *P. penetrans.*

Potato biomass assay: Potatoes were dug with a potato research harvester developed by the MSU Department of Agricultural Engineering. Tubers were graded as follows: J-size can not pass through a circle with a diameter of 8.25 cm; B-size can pass through a crevasse with a width of 4.8 cm; and A-size between the J-size and B-size tubers. Total tuber yield was expressed as weight in metric tons per hectare.

Data analysis: Pathogen population densities were transformed to ln $(x + 1)$ values for analysis of variance procedures and mean separation tests. Differences among treatment means were determined according to Tukey's Honestly Significant Difference test ($P < 0.05$). Single-degree-of-freedom comparisons were used to compare the cropping regimes. Tuber yields were regressed on the following variables: *P. penetrans* alone; *V. dahliae* alone; *P. penetrans* and *V. dahliae;* and *P. penetrans, V. dahliae* and *P. penetrans* × *V. dahliae.* A regression model was used to test the hypothesis that *P. penetrans* and *V. dahliae* would have similar effects on potato yields across all cropping regimes, but the constant would be different due to the different soil environments induced by the various cropping regimes. This model had 12 parameters, 10 constants (1 for each cropping regime), a single coefficient for *P. penetrans* and a single coefficient for *V. dahliae.* A series of *t* tests were used to determine which constants were more similar to each other. Non-transformed *P. penetrans* and *V. dahliae* densities were used for these regression models.

Results

A single year of rotation with corn, sudax, sweet clover, and alfalfa in 1989 resulted in 1990 potato tuber yields of 30.2, 26.0, 28.2, and 29.3 ton/ha, respectively, not different from 28.0 ton/ha after 2 years of continuous potato production ($P < 0.05$). In 1991, total tuber yields from 1 year of corn, sudax, sweet clover, and alfalfa rotation followed by 2 years of potatoes were not different from that of 3-year potato monoculture ($P < 0.05$). Two years of sweet clover or alfalfa, however, resulted in increased potato tuber yields compared with 3-year potato monoculture ($P < 0.05$) (Table 1). Yields of A and B-size tubers were similar to those of total tuber yield, and the B-size tuber yield from the alfalfa-alfalfa-potato cropping regime was greater than all of the other nine cropping regimes except the clover-clover-potato regime ($P < 0.05$). Tuber yields from the continuous potato regime were better than 2 years of grain followed by potato and worse than 2 years of legumes followed by potato ($P < 0.05$). Two years of legumes resulted in greater potato tuber yields than the cropping regimes with 2 years of grains ($P < 0.05$).

The highest preplant population density of *V. dahliae* (34 cfu/g soil), coupled with a *P. penetrans* population density of 12/100 cm^3 soil, was observed in the sudax-sudax-potato cropping regime (Table 2) which also resulted in the lowest total and A-size tuber yield (Tables 1, 2). The highest preplant *P. penetrans* population density (54/100 cm^3 soil), coupled with a *V. dahliae* population density of 19.5 cfu/g soil, was observed in the corn-corn-potato cropping regime which resulted in the second lowest potato yield in 1991. Both the 2-year legume and 2-year grain rotations with potato resulted in lower *P. penetrans* population densities following potato compared

TABLE 1. Potato tuber yields associated with 10 3-year cropping regimes in a field infested with *Pratylenchus penetrans* and *Verticillium dahliae.*

Cropping regimes	Tuber yield (ton/ha)			
	A-size	J-size	B-size	Total
Potato-potato-potato	20.44 cd[a]	2.31 ab	0.07 c	22.83 bc
Potato-rye-potato	22.11 c	2.01 ab	0.20 bc	24.32 b
Corn-potato-potato	23.25 bc	2.21 ab	0.09 c	25.55 b
Corn-corn-potato	17.91 cd	1.78 ab	0.10 c	19.80 bc
Sudax-potato-potato	18.51 cd	2.09 ab	0.06 c	20.66 bc
Sudax-sudax-porato	15.13 d	2.04 ab	0.14 bc	17.31 c
Clover-potato-potato	21.08 cd	2.11 ab	0.21 bc	23.40 bc
Clover-clover-potato	31.31 a	1.68 b	0.81 ab	33.80 a
Alfalfa-potato-potato	21.55 c	2.34 a	0.14 bc	24.02 b
Alfalfa-alfalfa-potato	29.36 ab	1.91 ab	1.07 a	32.34 a
Contrast (*F, P*)				
3-yr potato vs all others	1.7, 0.206	4.4, 0.044	2.5, 0.125	1.4, 0.237
3-yr potato vs 2-yr grains	5.8, 0.021	6.0, 0.019	0.1, nd	6.4, 0.016
3-yr potato vs 2-yr legumes	36.9, 0.000	9.9, 0.003	23.6, 0.000	36.6, 0.000
2-yr grains vs 2-yr legumes	108.1, 0.000	0.7, nd[b]	31.7, 0.000	110.2, 0.000

[a] Means followed by the same letter are not significantly different according to the Tukey's Honestly Significant Difference test ($P < 0.05$).
[b] Nd = not determined.

TABLE 2. Population densities of *Pratylenchus penetrans* and *Verticillium dahliae* associated with 10 3-year cropping regimes.

Cropping regimes	*V. dahliae* cfu/g soil 21 May '91	*P. penetrans*/100 cm^3 soil + 1-g root		
		21 May '91	28 June '91	20 Aug. '91
Potato-potato-potato	17.0 a[a]	9 b	106 ab	144 a
Potato-rye-potato	17.5 a	28 ab	143 ab	145 a
Corn-potato-potato	20.0 a	12 b	85 b	90 a
Corn-corn-potato	19.5 a	54 a	229 a	71 a
Sudax-potato-potato	23.5 a	13 b	191 ab	127 a
Sudax-sudax-potato	34.0 a	12 b	132 ab	70 a
Clover-potato-potato	16.5 a	16 b	201 ab	138 a
Clover-clover-potato	18.0 a	9 b	144 ab	67 a
Alfalfa-potato-potato	13.5 a	24 ab	154 ab	118 a
Alfalfa-alfalfa-potato	17.0 a	13 b	146 ab	67 a
Contrast (*F*, *P*)				
3-yr potato vs all others	0.3, nd[b]	4.4, 0.043	3.1, 0.085	4.0, 0.054
3-yr potato vs 2-yr grains	2.1, 0.153	14.6, 0.001	4.7, 0.037	8.0, 0.008
3-yr potato vs 2-yr legumes	<0.1, nd	0.1, nd	1.3, 0.261	8.7, 0.005
2-yr grains vs 2-yr legumes	2.9, 0.098	18.0, 0.000	1.6, 0.217	<0.1, nd

[a] Means followed by the same letter are not significantly different according to the Tukey's Honestly Significant Difference test ($P < 0.05$).
[b] ND = not determined.

with 3 years of continuous potato ($P < 0.01$) (Table 2). *Pratylenchus penetrans* populations in 1991, preplant and midseason, were higher in the 2-year crop rotation with potato than in most other cropping regimes ($P > 0.05$) (Table 2). *Pratylenchus penetrans* densities were lower in continuous potato compared with all other cropping regimes at the beginning of the season, but the differences were smaller at the midseason and harvest sampling dates. At harvest, the continuous potato cropping regime had more *P. penetrans* than the 2-year grains and the 2-year legumes. There was no difference in *P. penetrans* densities between the 2-year legume and the 2-year grain cropping regimes (Table 2).

Tuber yields (Y) were regressed on *P. penetrans* (n) alone ($Y = 33.26 - 3.27\,n$, $r^2 = 0.175$, $P = 0.002$); *V. dahliae* (f) alone ($Y = 33.31 - 3.23f$, $r^2 = 0.237$, $P < 0.001$); *P. penetrans* and *V. dahliae* ($Y = 40.77 - 2.97\,n - 3.02\,f$, $R^2 = 0.380$, $P < 0.001$); and *P. penetrans*, *V. dahliae*, and *P. penetrans* × *V. dahliae* ($Y = 46.71 - 5.26\,n - 5.22f + 0.84\,nf$, $R^2 = 0.386$, $P < 0.001$), where n = preseason *P. penetrans* population density (nematode/100 cm^3 soil) and f = preseason *V. dahliae* population density (cfu/g soil).

Another regression model was constructed to test the hypothesis that *P. penetrans* and *V. dahliae* would have similar effects on potato yields across all cropping regimes, but the constant for each regime would be different due to the different soil environments induced by the various rotation schemes. This model had 12 parameters, 10 constants (1 for each rotation scheme), a single coefficient for *P. penetrans* and a single coefficient for *V. dahliae* (Table 3). The model had a much higher r^2 ($r^2 = 0.915$, $P < 0.001$) and was statistically more significant than the model for one constant ($F = 33.63$, $P < 0.01$).

A series of tests were run to determine which constants were more similar to each other. It was found that the rotation constant for continuous potato was similar to corn-corn-potato, sudax-potato-potato, sudax-sudax-potato, clover-potato-potato, and alfalfa-potato-potato (Table 4). The constant was significantly smaller than potato-rye-potato, corn-potato-potato, clover-clover-potato and alfalfa-alfalfa-potato. In this last group of four rotations, potato-rye-potato and corn-potato-potato

TABLE 3. Coefficients for a multiple regression model assuming a different constant for each cropping regime, but a similar effect across all regimes for *Pratylenchus penetrans* and *Verticillium dahliae* ($n = 50$, 38 df, $s^2 = 3.708$).

Variable	Coefficient	*P*
Pre-season *P. penetrans* population density (nematode/100 cm^3 soil)	−0.114	<0.001
Pre-season *V. dahliae* population density (cfu/g soil)	−0.172	<0.001
Potato-potato-potato constant	26.743	<0.001
Potato-rye-potato constant	30.478	<0.001
Corn-potato-potato constant	30.396	<0.001
Corn-corn-potato constant	29.234	<0.001
Sudax-potato-potato constant	26.189	<0.001
Sudax-sudax-potato constant	24.482	<0.001
Clover-potato-potato constant	28.028	<0.001
Clover-clover-potato constant	37.891	<0.001
Alfalfa-potato-potato constant	29.086	<0.001
Alfalfa-alfalfa-potato constant	36.760	<0.001

were not similar to clover-clover-potato and alfalfa-alfalfa-potato. However, the constants for clover-clover-potato and alfalfa-alfalfa-potato were not significantly different (*t* test, 38 df).

DISCUSSION

The results of this study indicated that at the Michigan State University Potato Research Farm in Entrican, Michigan, 1 year of rotation with corn, sudax, sweet clover, and alfalfa; or 2 years of the 2 grain crops had little impact on reducing potato early dying and increasing potato tuber yields. Two years of legumes followed by potato resulted in higher tuber yields, with a yield response equivalent to application of a nematicide for control of the premature potato vine death and subsequent tuber yield loss (2). *Pratylenchus penetrans* population densities were lower following 3-year cropping regimes than following a 3-year potato monoculture. Rowe et al. (23) suggested that although short 2- or 3-year rotation practices alone do not result in effective control of potato early dying, they are useful in the total potato production system.

Nitrogen availability is the cultural factor that has been most commonly associated with potato early dying disease. When nitrogen is less available to the plant's root system because of leaching or poor distribution, disease incidence and severity may increase (23). The increase we observed in tuber yields following 2-years of legumes may have been due to increased nitrogen availability, or possibly currently unidentified microbial factors.

Preplant inoculum densities of *P. penetrans* and *V. dahliae* reflected the host status of the plants grown the year before. Francl et al. (9) constructed regression and discriminant function models relating preplant soil population levels of both pathogens to tuber yield. The minimum number of fungus propagules necessary to cause at least a 10% yield reduction in the absence of the nematode was 11–18 cfu/cm^3 soil. Our 1991 preplant *V. dahliae* population densities were 13.5 − 34.0 cfu/g soil. Biotic and abiotic factors might modify the relationship between inoculum density and disease development (23). The regressions produced the best fit when potato tuber yields were regressed on both *V. dahliae* and *P. penetrans* population densities.

Interactions between nematodes and soilborne fungi have received considerable attention (1,21). Synergistic interactions between *V. dahliae* and *P. penetrans* in development of potato early dying have been reported (17,22,23,24). Recent work indicated that the impact of *M. hapla* on yield could be additive with *V. dahliae* (15). Additional research is needed on the nature of *V. dahliae-P. penetrans* interactions in the agroecosystem involving potato.

There has been little research on the effect of combined infection by these pathogens on tuber quality (16). More B-size tubers were recovered in 2-year legume ro-

TABLE 4. *T* statistic comparison of regression model constants for 10 cropping regimes.

Cropping regime	PPP	PRP	CPP	CCP	SPP	SSP	ClPP	ClClP	APP	AAP
PPP	0.000[a]	−2.857	−2.987	−1.507	0.450	1.761	−1.044	−9.151	−1.825	−8.191
PRP	***	0.000	0.064	0.904	3.338	4.429	1.954	−5.666	1.137	−4.941
CPP	***	***	0.000	0.727	3.446	4.679	1.934	−6.134	1.033	−5.215
CCP	***	***	***	0.000	1.910	2.843	0.784	−5.235	0.104	−4.763
SPP	***	***	***	***	0.000	1.371	−1.492	−9.525	−2.266	−8.609
SSP	***	***	***	***	***	0.000	−2.735	−10.500	−3.375	−9.544
ClPP	***	***	***	***	***	***	0.000	−8.008	−0.853	−7.158
ClClP	***	***	***	***	***	***	***	0.000	6.846	0.925
APP	***	***	***	***	***	***	***	***	0.000	−6.120
AAP	***	***	***	***	***	***	***	***	***	0.000

Regression model constants were compared with *t* statistics calculated as $(B_1 - B_2)$/square root $(d * s^2)$, where $d = c'M^{-1}c$ $(M = X'X)$.

Cropping regimes abbreviated as follows: PPP, potato-potato-potato; PRP, potato-rye-potato; CPP, corn-potato-potato; CCP, corn-corn-potato; SPP, sudax-potato-potato; SSP, sudax-sudax-potato; ClPP, clover-potato-potato; ClClP, clover-clover-potato; APP, alfalfa-potato-potato; AAP, alfalfa-alfalfa-potato.

[a] Constant comparison is significantly different at the $P < 0.05$ level if $t \leqq -2.1$ or $t \geqq 2.1$.

tations with potato and were highly correlated with the presence of *V. dahliae* and *P. penetrans* at the beginning of 1991 season. Because of the economic significance of tuber quality, additional research is needed on this topic.

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