Journal of Nematology 30(1):100–107. 1998.

Effect of Initial Nematode Population Density on the Interaction of *Pratylenchus penetrans* and *Verticillium dahliae* on 'Russet Burbank' Potato[1]

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Abstract: Four similar growth chamber experiments were conducted to test the hypothesis that the initial population density (Pi) of *Pratylenchus penetrans* influences the severity of interactive effects of *P. penetrans* and *Verticillium dahliae* on shoot growth, photosynthesis, and tuber yield of Russet Burbank potato. In each experiment, three population densities of *P. penetrans* with and without concomitant inoculation with *V. dahliae* were compared with nematode-free controls. The three specific Pi of *P. penetrans* tested varied from experiment to experiment but fell in the ranges 0.8–2.5, 1.8–3.9, 2.1–8.8, and 7.5–32.4 nematodes/cm^3 soil. Inoculum of *V. dahliae* was mixed into soil, and the assayed density was 5.4 propagules/gram dry soil. Plants were grown 60 to 80 days in a controlled environment. Plant growth parameters in two experiments indicated significant interactions between *P. penetrans* and *V. dahliae*. In the absence of *V. dahliae*, *P. penetrans* did not reduce plant growth and tuber yield below that of the nematode-free control or did so only at the highest one or two population densities tested. In the presence of *V. dahliae*, the lowest population density significantly reduced shoot weight and photosynthesis in three and four experiments, respectively. Higher densities had no additional effect on shoot weight and caused additional reductions in photosynthesis in only one experiment. Population densities of 0.8 and 7.5 nematodes/cm^3 soil reduced tuber yield by 51% and 45%, whereas higher densities had no effect or a 15% additional effect, respectively. These data indicate that interactive effects between *P. penetrans* and *V. dahliae* on Russet Burbank potato are manifested at *P. penetrans* population densities less than 1 nematode/cm^3 soil and that the nematode population density must be substantially higher before additional effects are apparent.

Key words: concomitant populations, disease complex, fungus, interaction, lesion nematode, nematode, potato, potato early dying, *Pratylenchus penetrans*, root-lesion nematode, *Solanum tuberosum*, *Verticillium dahliae*, Verticillium wilt.

The root-lesion nematode, *Pratylenchus penetrans*, is endemic to potato (*Solanum tuberosum*) production areas in the northeastern United States and Canada (Townshend et al., 1978). Studies using controlled inoculum densities of *P. penetrans* demonstrated reduced tuber yields for nematode-infected potato cultivars Sebago (Olthof and Potter, 1973), Yukon Gold, Monona, Norchip (Olthof, 1986), Superior (Bernard and Laughlin, 1976; Olthof, 1986), Katahdin (Bernard and Laughlin, 1976), Kennebec (Bernard and Laughlin, 1976; Olthof, 1986), Voran (Oostenbrink, 1958), and Russet Burbank (Olthof, 1983, 1986). Enhanced yields in infested fields treated with nematicides are also evidence of the pathogenicity of *P. penetrans* to Superior potato (Kimpinski and McRae, 1988; Vitosh et al., 1980).

A synergistic interaction of *P. penetrans* and *Verticillium dahliae* has been demonstrated to reduce yields and tuber quality of both Superior (Botseas and Rowe, 1994; Martin et al., 1982; Rowe et al., 1985) and Russet Burbank (MacGuidwin and Rouse, 1990) potato. In field (MacGuidwin and Rouse, 1990; Wheeler et al., 1994) and microplot (Kotcon et al., 1985; MacGuidwin and Rouse, 1990; Rowe et al., 1985) studies, initial inoculum densities of the nematode and fungus too low to cause a deleterious effect alone caused foliar symptoms and reduced yield when present together.

Yield of Superior potato grown in soil infested by both *V. dahliae* and *P. penetrans* was more responsive to changes in the initial inoculum density of the fungus than to that of the nematode (Rowe et al., 1985). Using data from this and subsequent studies, Francl et al. (1987) developed a predictive

Received for publication 11 February 1997.

[1] Supported by a grant from the USDA NRI (#92-3702-7609) and funds from the Wisconsin Potato and Vegetable Growers Association.

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The authors thank Thomas Sharkey for advice, Murray Clayton for statistical consulting, and Steve Vicen for assistance in figure preparation.

model that linearly related yield loss of Superior potato to the logarithm of the product of *V. dahliae* and *P. penetrans* population densities at planting. Francl et al. (1987) noted that his model assumed equivalence of the fungus and nematode in the interaction. Wheeler et al. (1992) followed with a model that excluded *P. penetrans* density as a separate algebraic term in the model but which included a minimum relative yield term, the value of which differed depending on the presence or absence of *P. penetrans*. Their model was based on 5 years of yield data from microplots infested with 0 to 5 *P. penetrans*/cm^3 soil. Bernard and Laughlin (1976) also observed a limit in the yield reduction of Superior potato infected with only *P. penetrans*. In their study, initial inoculum densities (Pi) of 38 and 210 nematodes/100 cm^3 soil gave similar reductions in yield of Superior potato.

There are insufficient data on the relationship between initial nematode densities and yield of Russet Burbank potato infected with *V. dahliae*. In one study, plants grown in microplots infested with *V. dahliae* yielded less and displayed more severe early dying disease symptoms at 68 than at 27 *P. penetrans*/100 cm^3 soil (MacGuidwin and Rouse, 1990). In two field trials conducted in different years, there was a significant negative linear relationship between *P. penetrans* Pi and potato yield in soil infested with *V. dahliae* one year, but not the other (MacGuidwin and Rouse, 1990). Two other studies (Bernard and Laughlin, 1976; Kimpinski and McRae, 1988) did not demonstrate a relationship between Pi of *P. penetrans* and potato yield when the fungus was not present.

The objective of our study was to determine the impact of the initial population density of *P. penetrans* on Russet Burbank potato, with and without *V. dahliae*. We were interested in whether the interactive effect of the nematode and fungus varied according to number of nematodes present. This information is important for designing nematode management strategies for potato early dying disease and to help understand the nature of this nematode-fungus interaction.

Materials and Methods

Four experiments were conducted in a controlled plant growth facility from January 1993 to April 1994. Treatments were three inoculum levels of *Pratylenchus penetrans*, alone and in combination with one level of *Verticillium dahliae*, *V. dahliae* alone, and an uninfested control. The treatment structure and experimental design (randomized complete block with four replications) were common to all experiments, but the nematode inoculum level varied among experiments (see Table 1 for initial population densities).

Russet Burbank potato was propagated from tissue culture stock and planted either as sprouted microtubers in pasteurized Plainfield loamy sand soil (92% sand, 5% silt, 3% clay; <1% organic matter) (experiment 1) or as potato plantlets in a 1:1 (v:v) mix of pasteurized Plainfield loamy sand soil and vermiculite (experiments 2–4). Each plant was grown in a 20-liter plastic pot and produced a single main stem that was staked upright.

A Wisconsin isolate of *V. dahliae* (WI V-18, vegetative compatibility group 4a sensu Joachim and Rowe (1991)) was grown on sterile rye seed at 20 °C for 5 weeks. The culture was dried and ground in a Wiley Mill and assayed by dilution plating to contain 1×10^6 propagules/g rye seed. The ground inoculum of *V. dahliae*, applied at a rate of 0.5 g/liter soil mix, was thoroughly incorporated by hand into soil before it was added to the pots. Assays of the infested soil detected 5.4 propagules of *V. dahliae*/g soil. Ground rye seed only was added to pots not assigned to the *V. dahliae* treatments.

A Wisconsin isolate of *Pratylenchus penetrans* was cultured on root explant cultures of I. O. Chief sweet corn grown on Gamborg's B-5 medium without auxins or cytokinins. Nematode inoculum was collected (Layne and MacGuidwin, 1989); counted; apportioned into low, moderate, and light levels; and each of these counted again to

TABLE 1. Fresh shoot weight, tuber weight, and area under the carbon assimilation rate (photosynthesis) curve (AUAC) for four growth chamber experiments with zero, low, medium, and high initial population densities of *Pratylenchus penetrans* with (+) and without (–) *Verticillium dahliae* (Vd).

Treatment[a]	Shoot weight (g)		Tuber weight (g)		Photosynthesis index	
	–Vd	+Vd	–Vd	+Vd	–Vd	+Vd
			Experiment 1			
Control	137 a	114 a	300 a	312 a	864 a	861 a
Low (7.5)	137 a	78 b	297 a	171 b	937 a	593 b
Medium (14.6)	151 a	82 b	272 a	148 bc	651 b	306 c
High (32.4)	154 a	92 b	225 b	126 c	795 ab	368 c
Nematode effect	$P = 0.10$		$P = 0.001$		$P = 0.001$	
Verticillium effect	$P = 0.001$		$P = 0.001$		$P = 0.001$	
Interaction	$P = 0.02$		$P = 0.001$		$P = 0.01$	
			Experiment 2			
Control	696 a	582 a	828 a	866 a	322 a	288 a
Low (0.8)	626 a	204 c	875 a	428 bc	294 ab	156 b
Medium (1.8)	676 a	301 b	964 a	559 b	304 ab	174 b
High (2.5)	690 a	198 c	782 a	407 c	269 b	132 b
Nematode effect	$P = 0.001$		$P = 0.001$		$P = 0.001$	
Verticillium effect	$P = 0.001$		$P = 0.001$		$P = 0.001$	
Interaction	$P = 0.001$		$P = 0.001$		$P = 0.001$	
			Experiment 3			
Control	171 a	168 a	238 a	186 a	174 a	152 a
Low (2.1)	177 a	140 ab	187 ab	130 a	156 a	86 b
Medium (3.9)	168 a	135 ab	153 bc	127 a	176 a	109 ab
High (8.8)	129 a	119 b	107 c	49 b	175 a	131 ab
Nematode effect	$P = 0.02$		$P = 0.001$		$P = 0.09$	
Verticillium effect	$P = 0.04$		$P = 0.01$		$P = 0.001$	
Interaction	NS		NS		NS	
			Experiment 4			
Control	2,179 a	1657 a	518 ab	372 a	163 a	124 a
Low (1.3)	1,848 ab	1036 c	653 a	466 a	130 ab	65 b
Medium (2.7)	1,759 b	1293 bc	662 a	500 a	123 b	90 ab
High (4.1)	1,924 ab	1434 ab	400 b	428 a	115 b	67 b
Nematode effect	$P = 0.001$		$P = 0.01$		$P = 0.001$	
Verticillium effect	$P = 0.001$		$P = 0.001$		$P = 0.001$	
Interaction	NS		NS		NS	

[a] The mean number of nematodes added per treatment appears in parentheses.
[b] Experiments 1, 2, 3, and 4 were terminated 63, 80, 60, and 70 days, respectively, after inoculating potato plants.

estimate the number of nematodes delivered per pot (Table 1). Nematode inoculum was added when potato microtubers (experiment 1) or plantlets (experiments 2–4) were transplanted. For experiment 1, the nematode inoculum was thoroughly mixed into soil by hand before it was added to the 20-liter pots. For experiments 2 to 4, nematode inoculum was added around the sides of a cylindrical depression made when the 20-liter pots were only partially filled with soil mix. The nematode inoculum was squirted onto the sides of the depression with a syringe, the potato transplant was positioned, and the remaining soil mix added. Corn explant cultures without nematodes also were rinsed with water, which was then added to pots not assigned to the *P. penetrans* treatments.

Plants were maintained in growth rooms under light supplied by cool white fluorescent and incandescent lamps with a photoperiod of 14 hours. Relative humidity was maintained at 50 ± 5%. Day temperature was 25 ± 0.5 °C, and night temperature was 15 ± 0.5 °C. Plants were automatically watered to excess with quarter-strength Hoagland's solution twice daily for the first 2 weeks and then four times daily thereafter.

Twenty days after transplanting, the youngest fully expanded leaf from each plant was tagged, and its carbon assimilation

rate was measured with a LI-6200 portable photosynthesis system (LI-Cor, Lincoln, NE). On seven to nine additional dates, depending on the experiment, a new leaf was tagged and carbon assimilation measurements were collected on that and all previously tagged leaves. Leaves tagged on a particular date were designated as a cohort for the purpose of data analysis.

Experiments 1, 2, 3, and 4 were terminated 63, 80, 60, and 70 days, respectively, after transplanting the plants into infested soil. Shoots were severed at the soil surface and weighed. Roots, stolons, and the portion of the stem below the soil surface were shaken to remove soil and weighed collectively. Tubers were weighed separately. Relative tuber yield for each treatment and experiment was calculated by dividing the total weight of the tubers per pot by the average tuber weight for the uninfested (control) treatment.

All plants were assayed for *V. dahliae* and *P. penetrans* within 1 week after harvest. Stem colonization by *V. dahliae* was detected by incubating 0.1 ml of sap squeezed from a 3- to 5-cm piece of stem cut at the soil line on a semi-selective medium in petri dishes. The dishes were examined 2 weeks later for colonies of *V. dahliae.* After weighing the entire root system, roots were cut into pieces ca. 1 cm long, mixed, and a 2-g subsample removed for nematode assay on Baermann funnels for 2 days. A 100-cm^3 soil sample was collected after the soil was removed from pots, thoroughly mixed, and assayed for *P. penetrans* with a centrifugation-incubation technique (Jenkins, 1964). Counts of *P. penetrans* were adjusted for the extraction efficiency of the soil and root assay procedures (MacGuidwin, 1989). The total number of nematodes present per pot was calculated based on soil volume and root weight.

Shoot and tuber weights, counts of *P. penetrans* and *V. dahliae,* and an index of photosynthesis were analyzed for each experiment with an analysis of variance by means of the GLM procedure of SAS (SAS Institute, Cary, NC) for two factors (fungus and nematode) with two (*Verticillium*) or four (nematode) levels. The index of photosynthesis was computed by plotting the assimilation rate of each leaf cohort against time, calculating the area under the curve by integration, and summing the values into a single statistic that described the photosynthetic capacity of each potato plant. Regression analysis was used to detect linear trends in the response variables to increasing initial inoculum doses of *P. penetrans;* separate analyses were conducted for the nematode alone and the nematode + fungus treatments.

Shoot weight and carbon assimilation data from the growth chamber experiments were used to estimate the relative importance of two factors that determine potato tuber yields—reduced light interception versus reduced light use efficiency. The proportional radiation intercepted (RI) by each plant was calculated by subtracting the radiation energy measured for the oldest leaf cohort (the leaf most shaded by the plant canopy) from the amount of incident radiation. It was assumed that photosynthetically active radiation in the growth chamber was equivalent to solar radiation if multiplied by a factor of 0.5 (Technical Reference Manual for LI-6200, Li-Cor, Lincoln, NE) and that the amount of incident radiation available was equal to the value obtained in the photosynthesis measurements for the youngest leaf cohort. The proportional radiation use efficiency (RUE) of each plant was calculated by averaging the assimilation rate of all leaf cohorts collected during the experiment and dividing by the maximum assimilation rate measured during the same experiment. An empirical value of 1.4, derived by Monteith (1977), was multiplied by the RUE to predict the dry matter production of potato in grams per square meter per day. These daily values were multiplied by the number of days in each experiment to calculate the accumulation of biomass based only on reduced light use efficiency. The RI values were multiplied by the RUE values to account for the combined effects of radiation interception and light use efficiency on potato dry matter accumulation. The effect of RI alone on potato dry matter accumulation was calculated as the difference be-

tween these two estimates. Predicted dry matter production in grams per square meter was converted to a grams-per-plant basis by a multiplication factor of 0.0729, the estimated area covered by each potted potato plant. The average total loss predicted for every pathogen treatment relative to the noninoculated control was compared to the data collected for tuber fresh weight by regression analysis.

Results and Discussion

For all experiments, the most pronounced and consistent differences among treatments for all response variables were in comparisons of control, *V. dahliae* without *P. penetrans,* low *P. penetrans* without *V. dahliae,* and low *P. penetrans* with *V. dahliae* treatments (Table 1). The lowest nematode Pi in the absence of *V. dahliae* did not reduce shoot weight, tuber weight, or photosynthetic capacity below that of control plants in any experiment. The lowest nematode Pi in the presence of the fungus had a deleterious effect greater than that caused by *V. dahliae* infection alone for shoot weight in three experiments, tuber weight in two experiments, and photosynthesis index in all four experiments. In all cases, mean values for the low nematode dose + *V. dahliae* treatments were reduced below that of the corresponding single pathogen treatments more than would be expected if the effects of the nematode and fungus were additive. This synergistic response of potato to concomitant infection by *P. penetrans* and *V. dahliae* is predictable and highly repeatable, based on a number of independent studies (Botseas and Rowe, 1994; Francl et al., 1987; Kotcon et al., 1985; MacGuidwin and Rouse, 1990; Martin et al., 1982; Rowe et al., 1985; Wheeler et al., 1994).

For plants infected with both *P. penetrans* and *V. dahliae,* the additional impact of increasing nematode Pi beyond the lowest population density tested varied depending on the range of Pi used. Increasing nematode Pi caused incremental reductions in tuber weight for experiment 1, which tested Pi values ranging from 7.5 to 32.4. In experiment 3 there was a twofold reduction in tuber weight between the low Pi of 2.1 and the high Pi of 8.8, but the intermediate Pi tested caused no additional yield loss. Adding two to three times more nematodes in experiment 2 caused no additional yield loss beyond that noted for the lowest Pi of 0.8. There were no treatment effects on yield in experiment 4, which was not unexpected because plants in this experiment produced an unusual amount of shoot growth and secondary branching, which may have compensated for the deleterious interactive effects of *P. penetrans* and *V. dahliae* on premature leaf senescence.

Wheeler et al. (1992) found that yield loss of Superior potato was proportional to the inoculum level of *V. dahliae* and only qualitatively related to the presence of *P. penetrans.* Their data set included densities of 0.1 to 1.65 nematodes/cm^3 soil, a range similar to the low range we used in experiment 2. Our results for that experiment are consistent with their model. The fact that we found yield loss to reflect nematode Pi at higher nematode densities in the presence of *V. dahliae* indicates the model needs to be refined before it is used as a basis for nematode management decisions.

The model proposed by Wheeler et al. (1992) to describe the interactive effects of *P. penetrans* and *V. dahliae* was not based on symptom expression. However, our data for the photosynthesis index are consistent with their model for all of the ranges of nematode Pi we tested. The only significant linear trend in the index of photosynthesis was for the nematode-only treatments in experiment 4 (Table 1). Our data for an array of physiological parameters on a single data (Saeed et al., 1997b) and for physiological-based symptom expression over time (Saeed et al., 1997a) for experiments 2 and 4 also showed that the most severe plant response was not always associated with the highest Pi.

Our analysis of RI and RUE effects for experiment 2 indicates that the impact of the *P. penetrans-V. dahliae* interaction on plant biomass is due to more than just compromised plant growth or leaf senescence (Fig. 1). Estimated losses for total plant dry mat-

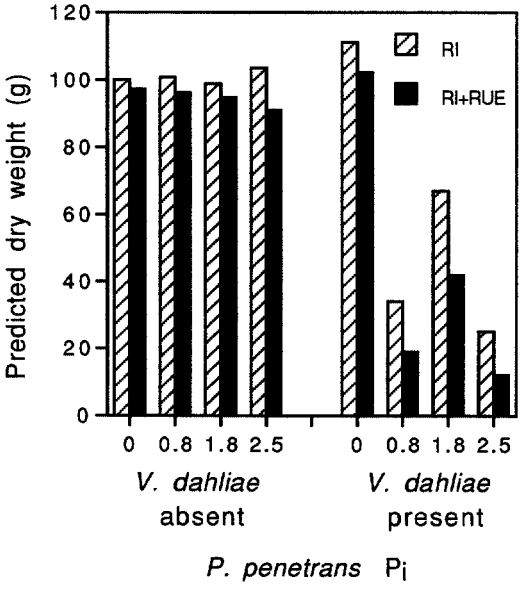

FIG. 1. Estimated potato plant dry weight for plants infected with four initial population densities of *Pratylenchus penetrans* (0, 0.8, 1.8, and 2.5 nematodes/cm^3 soil) grown for 80 days (experiment 2) in soil infested with 0 (*V. dahliae* absent) or 5.4 propagules/gram soil (*V. dahliae* present) of *Verticillium dahliae,* considering only the effect of each treatment on the amount of radiation intercepted (RI) by plants or considering both the radiation intercepted and the efficiency of plants to use the intercepted radiation (RUE).

ter accumulation were correlated with measured reductions in fresh tuber + shoot weight for three of the four experiments: $R^2 = 0.80$ ($P = 0.01$), 0.99 ($P = 0.0001$), 0.17 ($P = 0.20$), and 0.43 ($P = 0.07$) for experiments 1 to 4, respectively. There was little predicted effect of *V. dahliae* or *P. penetrans* alone on plant biomass, but the combination treatments averaged 75% less predicted total biomass (actual = 54%) than the control. An estimated 73% of this loss was attributable to reduced radiation interception by plants and 27% to reduced gas exchange. These values are similar to those calculated by Bowden and Rouse (1991) for potato grown in *V. dahliae*-infested soil without *P. penetrans.*

The close agreement of our results with those of Bowden and Rouse (1991) and the similarity in estimated RUE effects for plants exposed to inoculum densities of 0.8 and 2.5 *P. penetrans*/cm^3 soil indicate that the interactive effects of *P. penetrans* and *V. dahliae* on foliar disease expression are due primarily to the activity of *V. dahliae.* Two greenhouse studies, one on tomato (Conroy et al., 1972) and one on potato (Rotenberg, 1997), found that *P. penetrans* infection increased the incidence of plants infected with *V. dahliae.* It has been proposed that nematodes enhance germination of *V. dahliae* microsclerotia (Bowers et al., 1996), provide entry points for infection (McKeen and Mountain, 1960), or delay or diminish host responses that impede the movement of the fungus into xylem vessels (Evans, 1987). Any function that accelerates the entry of the fungus into the vascular system could be invariant to nematode density because only a small number of successful invasions are necessary for the fungus to systemically colonize xylem vessels of Russet Burbank potato (Perry and Evert, 1983).

Without *V. dahliae,* nematode population densities of up to 2.7 *P. penetrans*/cm^3 soil did not reduce yields in experiments 2, 3, and 4. Bernard and Laughlin (1976) similarly found that 2.1 or fewer *P. penetrans*/cm^3 soil did not damage Russet Burbank potato grown in microplots. Tests for linearity further support a threshold of about 2 *P. penetrans*/cm^3 for yield reduction of Russet Burbank potato. Experiments 1 and 3, with ranges of Pi above this level, both showed a negative linear relationship ($P = 0.05$) between nematode Pi and tuber weight for the nematode-only treatments (analysis not shown). Linearity was not verified statistically ($P = 0.20$) in experiment 1 when *V. dahliae* was present, but linear trends were apparent.

Nematode population density per root weight unit at the end of each experiment was related to Pi in experiments 3 and 4 and to the presence or absence of *V. dahliae* in experiments 2 and 4 (Table 2). Nematode population densities in roots were decreased by *V. dahliae* infection in experiment 2 and increased, at some inoculum levels, in experiment 4. *Verticillium dahliae* infection had a negative effect ($P = 0.001$) on the total number of nematodes per pot in experiment 2 and no effect in the other three experiments (data not shown). These data, in

TABLE 2. Number of *Pratylenchus penetrans* extracted from roots at the end of four experiments with different initial nematode population densities (Pi) per cm^3 soil, with (+Vd) and wihtout (–Vd) inoculation with *Verticillium dahliae* at 5.4 CFU/g dry soil.

	Pratylenchus penetrans/2 grams roots							
	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
Pi/cm^3	+Vd	–Vd	+Vd	–Vd	+Vd	–Vd	+Vd	–Vd
0.8			97	260				
1.3							43	13
1.8			95	211				
2.1					196	140		
2.5			110	196				
2.7							57	77
3.9					232	414		
4.1							163	27
7.5	132	77						
8.8					889	450		
14.6	147	157						
32.2	115	117						
Pp main effect[a]	NS		NS		0.02		0.01	
Vd main effect[a]	NS		0.01		NS		0.01	
Pp × Vd interaction	NS		NS		NS		0.01	

[a]Pp = *Pratylenchus penetrans;* Vd = *Verticillium dahliae.*

agreement with other studies (Burpee and Bloom, 1978; Conroy et al., 1972; Martin et al., 1982), failed to demonstrate a positive effect of the fungus on nematode reproduction. Russet Burbank potato is an excellent host for reproduction by *P. penetrans* (Bernard and Laughlin, 1976; Monteith, 1977), and, if our plants reached the carrying capacity for nematode population densities, an additional effect due to fungus infection might not be detected. Population densities of *V. dahliae* at harvest did not differ among treatments for three of the four experiments (data not shown). For experiment 3, counts of *V. dahliae* colony-forming units were higher ($P = 0.10$) for all nematode + fungus treatments than for the *V. dahliae*-only treatment.

Although our experiments demonstrated that high initial nematode population densities can have a greater impact on the growth and yield of *V. dahliae*-infected potatoes than low densities, the more important implication of our data is that sometimes they do not. Our study suggests that foliar symptoms are less sensitive to *P. penetrans* activity than tuber growth. A better understanding of the effects of *P. penetrans* on the biomass partitioning of potato plants may be necessary to refine our ability to predict yield loss due to the interactive effects of *P. penetrans* and *V. dahliae* in potato early dying disease.

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