Development of a Damage Function Model for *Pratylenchus penetrans* on Corn

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Abstract

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The lesion nematode *Pratylenchus penetrans* is a common pest of corn in the north-central United States. There are relatively few studies documenting the impact of *Pratylenchus* spp. on grain yield even though they are recognized as pests of corn and the target of commercial seed treatments. We adapted a component error modeling approach to develop a damage function for *P. penetrans* that included the influence of year and site in the yield loss relationship. Field data from six site-years was used to derive panel data consisting of all pairwise comparisons of the difference in nematode population densities and the associated proportional yield difference. Fourteen regression models of the relationship between proportional yield loss and the difference in nematode density were developed from soil and root assays at different corn growth stages. Seven models were significant: four models based on nematode population densities in soil (initial and final samples) and three based on nematode densities in seminal roots (corn growth stages V1 to V2 and V6)

and adventitious roots (corn growth stage R1 to R2). The model we consider to be the most important, that based on the initial soil assay, estimated the yield loss caused by each nematode to be 0.0142%. The grand mean of the 118 plots we sampled implied a yield loss of 3.79%. The random effects of year and field did not contribute significantly to any of the models but were close to significance for some, suggesting a benefit from larger data sets. Experimental error was the largest component of the variance for all of the models; therefore, the damage function is more useful for demonstrating impact of *P. penetrans* rather than for accurately predicting yield loss at the field level. All of the fields in our study were an irrigated loamy sand soil, with grain yields above the county average; therefore, it is possible that our damage function is conservative. The value of soil sampling has been questioned for *P. penetrans* and this study shows it to be equal to if not better than root assays for predicting yield.

The lesion nematode *Pratylenchus* sp. is a very common pest in the north-central United States (Townshend et al. 1978). *Pratylenchus* was the first or second most common genus among plant-parasitic nematodes reported in censuses from Illinois (Mekete et al. 2011), Iowa (Tylka et al. 2011), Minnesota (Chen et al. 2012), and Wisconsin (MacGuidwin and Bender 2012). Population densities of lesion nematodes can build rapidly due to a very wide host range and a high capacity for surviving desiccation (Townshend 1984), as might be expected during periods of soil freezing and lack of rainfall.

Corn (*Zea mays* L.) is an excellent host to many *Pratylenchus* spp., including those common to the north-central United States, including *Pratylenchus penetrans* (Cobb) Filipjev & Schuurmans-Stekhoven (Dickerson et al. 1964), *P. scribneri* Steiner (Smolik and Wicks 1987; Todd and Oakley 1996), *P. hexincisus* Taylor & Jenkins (Smolik and Wicks 1987; Zirakparvar et al. 1980), *P. neglectus* (Rensch) Filipjev & Schuurmans Stekhoven (Todd and Oakley 1996), and *P. crenatus* Loof (Townshend et al. 1978). All vermiform stages feed ectoparasitically on root epidermal cells or as endoparasites in the root cortex causing necrotic lesions. Damage resulting from nematode feeding is related to population densities (Norton 1983), which can be estimated from soil and root samples at any time of year, including periods when no host is present and nematodes are sheltered in dead root fragments (MacGuidwin and Bender 2012).

Pratylenchus spp. are recognized widely in the popular press as pathogens of corn but there are relatively few studies formally documenting their impact on grain yield. Pathogenicity to corn grown indoors under controlled conditions was demonstrated for *P. penetrans* from Wisconsin (Dickerson et al. 1964) and *P. hexincisus* from Iowa (Waudou and Norton 1986). Field data from Iowa showed yield increases of 2 to 20% over 16 site-years when a suite of plant-parasitic nematodes, including *Pratylenchus* spp., were reduced by nematicides

(Norton et al. 1978). Pooled data from nematicide trials in South Dakota targeting *P. hexincisus* and *P. scribneri* (Smolik and Evenson 1987) and in Kansas targeting *P. scribneri* and *P. neglectus* (Todd and Oakley 1996) also showed significant relationships between nematode population densities and yield. The most recent of these studies was conducted in the mid-1990s, before genetically modified traits were available.

The empirical relationship between nematode population density and yield is mostly linear; therefore, regression approaches are commonly used to develop crop loss models (Barker and Olthof 1976). Initial inoculum was reported to be a good predictor of yield for many combinations of nematode pests and crops but was not useful for *Pratylenchus* spp. and corn in field studies. Negative linear relationships between population densities of *Pratylenchus* spp. in roots early (Todd and Oakley 1996) and midway (Smolik and Evenson 1987) in the season were predictive of yield. Significant relationships between the absolute number of *Pratylenchus* spp. and yield for corn (Smolik and Evenson 1987) and wheat (Nicol et al. 1999) using conventional regression implied that it might be possible to develop a damage function for *Pratylenchus* spp. using a nested component error modeling approach developed for corn rootworm (Dun et al. 2010; Mitchell et al. 2004; Tinsley et al. 2013).

Damage functions characterize the relationship between yield loss and a metric that captures the status of the pest population. We chose nematode population density in roots or soil for our models because it is information that farmers can obtain from a diagnostic lab at any point in the rotation cycle. Initially, damage functions paint a coarse picture of the relationship between nematode populations and crop loss that can be used to apprise farmers of nematodes, estimate the impact of nematodes to a region or crop, and analyze the average benefit of a nematicidal treatment to an industry. As more data become available over time, damage functions can be refined to include factors that make them more specific to local conditions. Component error modeling is one method for revealing factors with a strong influence on pest damage functions.

Component error models, originally developed to study the technical efficiency of instruments, have the advantage of calculating error estimates for specified factors separate from the overall estimate of experimental error, unlike conventional regression models that combine all sources of error into a single estimate. Antweiler (2001)

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developed a version of a component error model that accommodates data sets with factors that can be grouped in a hierarchy and are unbalanced for the number of observations, subgroups, or groups. Mitchell et al. (2004) and Dun et al. (2010) adapted the Antweiler model to describe damage functions for corn as predicted from corn root worm injury ratings across different locations and years, and Tinsley et al. (2013) applied their statistical analyses to a SAS (SAS Institute, Cary NC) platform. We used the methods described by these researchers to confirm the pathogenicity of lesion nematodes to current corn genotypes modified with transgenic traits of herbicide tolerance and insect resistance. We developed a damage function for *P. penetrans*, a species not considered in previous studies, including the influence of year and site to the yield loss relationship.

Materials and Methods

Data were collected from bulk-planted corn fields at the Hancock Research Station (HRS), Hancock WI, from 2008 to 2010 for a total of six field-years. The fields shared a common soil type (Plainfield loamy sand) and were managed for irrigated vegetable and potato production, including the practice of soil fumigation before potato crops. The fields were different for the previous crop (soybean, sweet corn, or field corn), the number of years since the last potato crop (range = 2 to 5 years), planting date (19 April to 19 May), and corn genotype. All corn hybrids were 97- to 99-day maturity, with glyphosate resistance and *Bacillus thuringiensis* toxin traits and planted at

a seeding rate of 14,500 seeds/ha. *P. penetrans* is endemic to the HRS but staff did not believe nematodes to be a threat to corn; therefore, no products or practices targeting nematodes were used. Weather records from HRS showed that 2008 and 2009 were cooler than the 30-year average and 2010 was warmer than average.

The first sampling date averaged 20 days after planting (140 to 215 degree-days, base 10°C), when the plants were at vegetative (V) growth stage V1 (two fields) or V2 (four fields). Random locations were flagged and stakes were placed 2 m on either side to demarcate a plot with dimensions of 1 row by 4 m. The number of plots in each field ranged from 16 to 25 and the number of fields sampled each year ranged from one to three (Table 1). Five plots were excluded in the data set for one field in 2010 due to experimenter error on the first sampling date. Soil samples were collected within each plot, close to the row but away from plants so as to exclude living roots from the sample. On subsequent dates, plants farthest from the flag on both ends of each plot were dug to a depth of 20 cm and brought to the lab for nematode assays. The calendar dates varied among years but sampling corresponded to corn growth stages V1 to V2, V3 to V4, V6, and V17 to R1, and reproductive (R) stages R2 to R4. Ears were harvested by hand at maturity (2 to 7 October) from the 5 plants on either side and closest to the flag (10 plants total) and soil samples were collected.

As a migratory endoparasite, *Pratylenchus* spp. can be recovered from dead root fragments, living roots, or soil year-round; therefore,

Table 1. Mean values and range of raw data from six site-years used in 14 models to estimate yield loss of corn due to *Pratylenchus penetrans*

Parameter ^a	2008	2009			2010	
	Field 1	Field 1	Field 2	Field 3	Field 1	Field 2
Number of plots	25	22	22	22	11 ^a	16
Yield (MT/ha)	12.2	9.6	11.3	9.9	10.2	8.9
Range	8.0–16.3	7.5–12.2	9.8–13.4	8.0–11.2	7.4–12.8	6.6–11.4
Growth stage V1 to V2						
100 cm ³ soil fraction only	55	61	42	85	115	13
Range	8–204	4–202	1–130	6–350	25–305	0–61
100 cm ³ total soil assay	103	305	184	263	1,076	32
Range	16–222	46–1,028	11–384	9–1,084	216–1,762	0–183
Nematodes g ⁻¹ (seminal)	789	3,556	657	4,945	4,563	65
Range	20–2,150	198–14,158	110–1,784	114–44,167	1,340–16,033	0–520
Nematodes g ⁻¹ (adventitious)	28	331	84	589	...	...
Range	0–300	56–1,146	0–438	0–2,550	0	0
Growth stage V3–V4						
Nematodes g ⁻¹ (seminal)	1,640	7,683	3,852	14,389	10,833	113
Range	300–5,136	1,141–26,821	775–13,810	149–47,101	586–32,567	0–567
Nematodes g ⁻¹ (adventitious)	835	1,521	506	2,305	893	71
Range	230–13,025	171–5,919	58–1,568	60–10,827	0–3,740	0–489
Growth stage V6						
Nematodes g ⁻¹ (seminal)	...	7,507	...	13,897	32,119	702
Range	...	521–77,312	...	384–47,918	6,571–61,800	0–5,400
Nematodes g ⁻¹ (adventitious)	...	61	...	128	1,077	37
Range	...	8–284	...	2–615	44–3,000	0–275
Growth stage V17 to R1						
Nematodes g ⁻¹ (seminal)	18,626	7,119	46,606	23,058	18,347	1,672
Range	400–54,429	50–27,818	1,556–255,209	393–118,000	5,556–29,900	0–18,440
Nematodes g ⁻¹ (adventitious)	170	39	106	132	1,079	22
Range	4–1,161	0–235	3–402	3–1,263	100–3,916	6–131
Growth stage R2 to R4						
Nematodes g ⁻¹ (seminal)	19,251	11,077	14,623	23,635	16,368	1,735
Range	40–52,800	256–51,792	625–36,329	383–58,356	2,667–31,667	0–11,323
Nematodes g ⁻¹ (adventitious)	59	764	122	222	2,056	139
Range	4–274	3–10,588	9–580	3–1,112	205–3,810	0–662
Harvest						
100 cm ³ soil fraction only	118	168	63	...	85	9
Range	31–877	2–398	12–192	...	60–98	0–30
100 cm ³ total soil assay	616	625	229	...	157	24
Range	173–2,631	46–1,028	34–392	...	60–287	1–88

^a Soil fraction only = nematodes recovered from the bulk soil (soil only) and total soil assay = nematodes recovered from the bulk soil plus root fragments contained therein. Seminal and adventitious roots were assayed separately.

a dual assay was used to quantify nematodes from soil samples (MacGuidwin and Bender 2012). Each sample was thoroughly mixed and added to a graduated cylinder containing water until the water was displaced by 100 ml. The sample, now in water, was placed in a pitcher and stirred vigorously to suspend nematodes and light fraction material and then decanted through a 250- μ m-pore sieve nested over a 38- μ m-pore sieve. Material retained on each sieve was assayed separately. Material caught on the 250- μ m-pore sieve was incubated on a Baermann Funnel for 48 h. Material caught on the 38- μ m-pore sieve was centrifuged in water to pellet the nematodes in the mineral fraction of the soil using methods similar to Jenkins (1964). Plant-parasitic nematodes were observed using a stereomicroscope from both assays. Nematodes were counted by genus and the counts from the two assays were combined to determine nematode population densities in 100 cm³ of soil and the root fragments contained therein (total soil assay). Verification of *P. penetrans* was based on morphological features of adult females, including three lip annules and a round, sperm-filled spermatheca, and the presence of males, features that distinguish *P. penetrans* from other species common to Wisconsin (Handoo and Golden 1989).

Plant samples were processed within 48 h of collection, with separate assays for the seminal and adventitious root systems. The seminal root system was separated by severing the mesocotyl right below the crown. The seed was removed but the mesocotyl retained for the assay. The roots were rinsed gently, blotted dry, cut into 1-cm pieces, and weighed. A 2-g subsample was placed on a Baermann funnel and incubated for 48 h. Nematodes were observed using a stereomicroscope and counted, with the presence of males noted. The root pieces were collected from the funnels, dried at 37°C, and weighed to calculate nematode population densities per gram (dry weight) for seminal and adventitious roots.

We developed unbalanced nested error component models from our data using techniques described by Dun et al. (2010) and Tinsley et al. (2013) for estimating yield loss from corn rootworm injury to roots. In our case, the independent variable was nematode population density and we made 14 models, 1 for each of the soil sample (two dates) and root sample (seminal and adventitious roots on five dates) data sets. The panel data consisted of all pairwise comparisons of the difference in nematode population densities and the associated proportional yield difference. For the first step in each analysis, the plot data within a field-year was sorted in ascending order of nematode population density and a matrix was constructed for calculating all pairwise comparisons for adjacent values. For plots *a* and *b* in the same field-year, the difference in nematode population density is $X_b - X_a$. The number of comparisons for each field-year is $n(n - 1)/2$ and the value is always positive. A second matrix was constructed of the proportional yield loss associated with each $X_b - X_a$ comparison. For plots *a* and *b* in the same field-year, the proportional yield difference is $(Y_a - Y_b)/Y_a$. The values for the yield difference can be either positive (yield loss is associated with increased nematode population density) or negative (yield gain is associated with increased nematode population density). The pairwise data from the six field-years were combined for a total of 1,168 data points in each model, except for five models where data were missing (adventitious roots at V1 to V2, seminal roots at V6, adventitious roots at V6, final soil fraction only, and final total soil assay).

Our model contained the random effects of year and field nested within year; therefore, we used PROC MIXED in SAS for Windows (SAS Institute Inc.) to estimate the relationship between proportional yield loss and the difference in nematode population density. The maximum-likelihood (ML) method was used to obtain estimates of the variance components and the covariance test option was used for parameter estimates. The solution option was used to estimate the fixed-effect of slope and intercept for the relationship between proportional yield loss and nematode population density difference and the Kenward-Rogers adjustment was specified for calculating the degrees of freedom for the denominator. Each model was first run with the fixed-effect intercept parameter to confirm that the effect was not significant and was then run again with the suppress intercept option to exclude the intercept. The rationale for forcing

the relationship to include the origin is that there should be no difference in proportional yield loss for plots with zero difference in nematode population density. The precedent for this decision was based on other applications of error component models (Dun et al. 2010; Mitchell et al. 2004; Tinsley et al. 2013). The contribution of the covariance parameters to model was determined by comparing partial models (one random effect) to the full model using ML ratio tests.

Results

Pratylenchus spp. were abundant in all of the fields, with fewer than 3% of the plots negative for nematodes. The predominant species was *P. penetrans*, with many males noted in all soil and root samples. The six site-year data sets showed a wide range of nematode population densities (Table 1). Fields fell into two categories for the mean soil initial population densities (P_i) estimated at corn growth stage V1 to V2: three fields had fewer and three fields had more than 200 nematodes per 100 cm³ of soil. Occasional (<10) specimens of *Paratrichodorus*, *Longidorus*, and *Xiphinema* were encountered, but *Pratylenchus* was the only genus common to all fields and *P. penetrans* was the most common species.

Population densities of nematodes (Table 1) were greater ($P < 0.05$) for seminal than adventitious roots for all fields and dates. Maximum root densities observed among sampling locations were 255,209 and 13,025 nematodes/g of root for seminal and adventitious roots, respectively (Table 1). The nematode reproductive factor (Rf) in roots, calculated as the ratio of nematodes per gram of root on the last versus the first sampling date, was greater for seminal roots (grand mean Rf = 32.5) than adventitious roots (grand mean Rf = 1.6). For the majority of fields, mean population densities of nematodes in roots over sampling dates fit a positive linear model for seminal roots and a quadratic model for adventitious roots (data not shown).

Seven composed error models based on a variety of sampling strategies showed a significant relationship between a gain in nematode density and proportional yield loss: soil fraction and total soil assays collected at V1 to V2 and harvest, seminal root assays collected at V1 to V2 and V6, and adventitious root assays collected at R2 to R4 (Table 2). All but the R2 to R4 model showed a significant positive increase in proportional yield loss as the difference in nematode population densities increased. The final estimates presented in Table 2 for the increase in yield loss with each additional nematode were obtained from model runs without the fixed effect of intercept. Prior runs showed the intercept term to be not significant, as would be expected given that the origin represents yield loss estimates from samples with zero difference in nematode population densities.

Figure 1 shows the model fit to data generated from total soil assays collected at V1 to V2. The estimate for the fixed effect of slope (Table 2) indicates that each nematode contributes a 0.0142% increase in yield loss. The average initial population density per plot was 267 nematodes per 100 cm³ of soil, which implies an average yield loss of 3.79% ($0.000142 \times 267 = 0.0379 \times 100$). Average yield loss for all plots suggested by the other models with the greatest *F* values for the fixed effect of slope ($P < 0.001$) were 2.77% for the soil fraction only at harvest (mean = 105 nematodes per 100 cm³ of soil) and 2.76% for the total soil assay at harvest (mean = 438 nematodes per 100 cm³ of soil). The yield loss estimates for each field suggested by all seven models are shown in Table 2.

The estimates for the random effects of year and field did not contribute significantly to the variance of the models (Table 3). The strongest contribution of year to the model was for the initial population density based on the total soil assay ($P = 0.12$). Field was almost significant for seminal roots at V1 to V2 ($P = 0.08$) and adventitious roots at R1 to R2 ($P = 0.053$). Experimental error was the largest component of the variance for all models, implying that a lot of the variability was not explained by differences among the fields within or across years. The parameter estimate for experimental error was 8-fold greater than year estimate for the total soil model, and 7- and 25-fold greater than the field estimate for the seminal root V1 to V2 and adventitious root R2 to R4 models, respectively.

Discussion

Our study confirms that *Pratylenchus* spp. are damaging to corn and expands the list of nematode yield loss models to include *P. penetrans* and corn hybrids improved for yield. The variables and damage function model we used to reach this conclusion were different from earlier studies, yet our yield loss estimates were in the range predicted for *P. scribneri* (Smolik and Evenson 1987) and *P. scribneri* and *P. neglectus* (Todd and Oakley 1996) in sandy soils of South Dakota and Kansas, respectively. We speculate that our estimate of 3.79% yield loss due to *P. penetrans* is conservative, given that the corn fields utilized in this study were not perceived to have pest problems, were managed using best practices, and achieved yields above the county average.

We consider the model based on the initial total soil assay to be the most useful for estimating the damage function of *P. penetrans* to corn. Although the soil sample was collected at corn growth stage V1 to V2, we purposely sampled midway between rows, approximately 30 cm from the corn seedlings, to obtain a sample that represented the nematode population at the time of planting. Theoretical (Seinhorst 1965) and empirical (Ferris 1984) critical point models for crop loss due to nematodes have been based on initial nematode population densities because the relationship is useful for making nematode management decisions as well as being statistically robust. Using a dual assay that included dead root fragments improved the damage function estimate relative to the soil assay only, validating our earlier conclusion (MacGuidwin and Bender 2012) that a significant fraction of lesion nematodes, including *P. penetrans*, shelter in dead roots of previous crops during the winter months in the northern corn belt.

We did not see a statistically significant contribution of field to our damage function models but some of the models were close to being significant at the $P = 0.05$ level. Damage function models based on soil samples collected at the start of the season appeared to be less influenced ($P = 0.28$ to 1.00) by the field factor than those based on soil samples collected at harvest ($P = 0.12$ to 0.13). Fields within a year were consistent for planting and sampling dates and management activities but varied for previous crop, number of years since fumigation, and corn genotype. Variation in pathogenicity among corn genotypes was demonstrated in a loamy sand field for *P. scribneri* (Waud and Norton 1986) and we have noted the same for *P. penetrans* (unpublished data). An impact of corn genotype on reproduction by *Pratylenchus* spp. has also been demonstrated (Smolik and Wicks 1987; Waud and Norton 1986) and would be expected to influence end-of-season population densities. Our data set did not include other location-sensitive variables known to affect the damage caused by *Pratylenchus* spp. such as soil type (Schmitt and Barker 1981); therefore, additional work is needed to determine the contribution these factors play in determining yield loss of corn caused by *P. penetrans*.

The random effect of year was almost statistically significant for the two models based on initial soil sampling ($P = 0.12$) but contributed virtually nothing to the other models. One factor that may account for the apparent differential role of year was a yearly change

in personnel responsible for sample collection and processing; nematode identification and enumeration was conducted by one person over the course of the study. Labor crews were less experienced in some years and interoperator variability may have had the greatest influence on data collected early in the season as employees trained. Given 3 years of data that were above and below 30-year temperature averages, we expected to see a strong year effect, but the fact that we didn't is consistent with other studies. Year was not a significant factor in explaining yield loss of corn infected with *P. scribneri* in Kansas (Todd and Oakley 1996) and studies manipulating water stress found no impact on the damage inflicted by *P. zeae* and *P. brachyurus* to corn (McDonald and Van den Berg 1993) or *P. penetrans* to apple (Jaffee et al. 1982). Three years of data are not sufficient to rule out the importance of seasonal influence on nematode damage to corn; therefore, we echo the call for large data sets (Dun et al. 2010; Tinsley et al. 2013) to develop damage functions.

The largest source of variability in all of our models was random experimental error. Potential sources of variability not accounted for by the effects of year and field within year include interoperator variability in sample collection and processing, corn genotype, other pests and diseases, and variation in soil characteristics at the subfield level. There were no obvious symptoms of harmful agents other than nematodes but it is possible that the cumulative effect of organisms operating at the subthreshold level was sufficient to affect corn yield. Variations in soil properties among the sampled areas we refer to as plots are highly likely, given that the fields were located at a research facility. Our data were collected in bulk-planted fields but, in other years, the fields were partitioned into fallow alleys and plots that were manipulated for crop genotype, pest pressure, or nutrient status. Nematodes, including *Pratylenchus* spp., show an aggregated distribution in all environments corresponding to variation in edaphic factors that also influence corn growth; therefore, corn yield data typically have a lot of unexplained variability, as illustrated by damage function models for corn rootworm larvae (Dun et al. 2010; Mitchell et al. 2004; Tinsley et al. 2013).

Fig. 1. Regression of proportional yield loss of corn and the difference in initial population density of *Pratylenchus penetrans* in soil.

Table 2. Maximum likelihood estimates of the slope and estimated yield loss of corn due to *Pratylenchus penetrans* for seven models

Model	Estimate ^a	SE ^b	<i>t</i>	<i>P</i>	Estimated yield loss for each site-year					
					2008	2009			2010	
					Field 1	Field 1	Field 2	Field 3	Field 1	Field 2
Soil fraction only, V1 to V2	2.43×10^{-4}	9.80×10^{-5}	2.48	0.0136	1.34	1.48	1.02	2.07	2.79	0.32
Total soil assay, V1 to V2	1.42×10^{-4}	2.90×10^{-5}	5.86	<0.0001	2.67	4.33	2.61	3.73	15.28	0.45
Seminal roots, V1 to V2	2.96×10^{-6}	1.07×10^{-6}	2.85	0.0045	0.23	1.05	0.19	1.46	1.06	0.02
Seminal roots, V6	6.03×10^{-7}	3.00×10^{-7}	1.98	0.0489	...	0.45	...	0.84	1.94	0.04
Adventitious roots, R2 to R4	-0.02×10^{-3}	3.61×10^{-6}	-6.89	<0.0001	0	0	0	0	0	0
Soil fraction only, harvest	2.64×10^{-4}	4.80×10^{-5}	5.45	<0.0001	3.12	4.45	1.67	...	2.25	0.24
Total soil assay, harvest	6.30×10^{-5}	1.80×10^{-5}	3.56	0.0004	3.88	3.94	1.44	...	0.99	0.15

^a Gain in proportional yield loss per nematode.

^b Standard error.

Nested error component models have been used in pest management to estimate damage functions for insects (Dun et al. 2010; Mitchell et al. 2004; Tinsley et al. 2013) but, to our knowledge, this is the first application of this approach for a nematode pest. We related yield to population densities of *P. penetrans* rather than to damage ratings, as has been the case for entomological models, because it is widely accepted that plant damage is proportional to nematode density and root necrosis can result from a variety of factors in addition to nematodes. Seinhorst (1965) developed a model based on Nicholson's competition curve (Nicholson 1933) which includes a slope-determining parameter to reduce the impact per nematode as population density increases. Over a wide range of values, the relationship is linear; therefore, many empirical models are based on linear regression of log-transformed population densities, which also implies that the damage per nematode declines as nematode population densities increase. Our damage function model differs from the Seinhorst model in that it is based on the pairwise difference in nematode numbers with no consideration for density-dependent effects. Some damage functions for *Pratylenchus* spp. are based on log-transformed values (Todd and Oakley 1996) and some on absolute nematode population densities (Franci et al. 1987; Nicol et al. 1999; Norton et al. 1978; Smolik and Evenson 1987); therefore, there is no empirical consensus on the need for building density dependency into models describing the impact of *Pratylenchus* spp. on corn. Data derived from sampling is often highly variable and transformations may improve model fit for this reason rather than pest biology. Seinhorst (1965) argues that the effect per nematode diminishes with increasing nematode population densities because of the overlap in nematode feeding sites. We propose that this may hold at a weak level or infrequently for *P. penetrans* injury

Table 3. Parameter estimates for the random effects of seven nested error component models estimating damage to corn from *Pratylenchus penetrans*

Model, effect	Estimate	Standard error	Wald Z value	Pa
Soil fraction only				
V1 to V2				
Year	4.200×10^{-3}	3.869×10^{-3}	1.09	0.139
Field (year)	3.560×10^{-4}	6.200×10^{-4}	0.57	0.283
Experimental error	2.943×10^{-2}	1.222×10^{-3}	24.09	<0.001
Total soil assay				
V1 to V2				
Year	3.798×10^{-3}	3.223×10^{-3}	1.18	0.120
Field (year)	0			NS
Experimental error	3.124×10^{-2}	1.294×10^{-3}	24.13	<0.001
Seminal roots				
V1 to V2				
Year	0	...	...	NS
Field (year)	1.490×10^{-3}	1.041×10^{-3}	1.43	0.076
Experimental error	3.683×10^{-2}	1.528×10^{-3}	24.10	<0.001
Seminal roots V6				
Year	1.112×10^{-4}	3.880×10^{-4}	0.29	0.386
Field (year)	3.320×10^{-4}	4.790×10^{-4}	0.69	0.244
Experimental error	1.230×10^{-2}	6.920×10^{-4}	17.78	<0.001
Adventitious roots				
R1 to R2				
Year	0	...	...	NS
Field (year)	4.025×10^{-3}	2.478×10^{-3}	1.62	0.052
Experimental error	2.939×10^{-2}	1.220×10^{-3}	24.10	<0.001
Soil fraction only harvest				
Year	0	...	...	NS
Field (year)	4.393×10^{-3}	3.961×10^{-3}	1.11	0.134
Experimental error	3.745×10^{-2}	1.888×10^{-3}	19.83	<0.001
Total soil assay harvest				
Year	0	...	...	NS
Field (year)	5.281×10^{-3}	4.500×10^{-3}	1.17	0.121
Experimental error	4.097×10^{-2}	2.095×10^{-3}	19.56	<0.001

^a NS = not significant.

to corn because nematodes can feed exterior to as well as inside roots and relocate throughout the entire life cycle, and are not restricted to a particular region along the root (Zunke 1990).

Our study demonstrates that the approach used by Mitchell et al. (2004) and others (Dun et al. 2010; Tinsley et al. 2013) estimating yield loss caused by corn rootworm damage is useful for *Pratylenchus* spp. By expressing damage as proportional yield loss, we were able to combine 6 data sets into one set of panel data, and others have merged as many as 19 (Tinsley et al. 2013), with the potential for many more due to the availability of statistical software capable of handling large unbalanced data sets. Modeling the difference in yield as a function of the difference in nematode population densities provided more estimates at both ends of the data range for independent variables. For example, the original data set contained 3 values of zero for the variable "total soil Pi" and represented one field, whereas the pairwise computation generated 13 values of zero that represented four fields, 3 years, and original data ranging from 0 to 232 nematodes per 100 cm³ of soil. Our study also illustrates the advantage of estimating variance components for random parameters. The two factors we hypothesized to be important were not statistically significant but they were nearly so, and the variation in their contribution among the models is interesting and amenable to empirical testing. The nearly significant contribution of the factors suggests that larger data sets might increase the likelihood that variability in proportional yield loss can be explained by year and location (field) and allows additional nested variables such as corn genotype, as described computationally by Antweiler (2001) and Dun et al. (2010).

The damage estimates suggested by our models are most suitable for evaluating the importance of *Pratylenchus* spp. to regional crop production and the general need for management tools. The high level of random unexplained experimental error decreases the utility of the estimates for accurately predicting yield loss at the field level. For the total soil model, the damage function suggests an average yield loss of 2.84% for samples with 195 to 205 nematodes per 100 cm³ of soil. Half of the pairwise comparisons showed a yield loss for this population density but the unexplained random variability was high, with the raw data ranging from a yield loss of 35% to a yield gain of 16%. It is likely that our damage function models could be improved by using larger data sets and including more fixed effects, as suggested by others (Dun et al. 2010; Mitchell et al. 2004; Tinsley et al. 2013). Although there is benefit in predicting yield loss accurately, the probability that some yield loss will occur and the bounds of the loss are important pieces of information used by farmers to guide management decisions.

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