

## RESEARCH

# Correlation between Soil pH, *Heterodera glycines* Population Densities, and Soybean Yield

P. Pedersen,\* G. L. Tylka, A. Mallarino, A. E. Macguidwin, N. C. Koval, and C. R. Grau

## ABSTRACT

Soybean cyst nematode (*Heterodera glycines* Ichinohe) is the most damaging pathogen of soybean [*Glycine max* (L.) Merr.] in the United States. Observations in fields suggest that high *H. glycines* population densities are associated with high soil pH, but *H. glycines* and soil pH have not been linked to soybean yield. The objective of our study was to assess the relationship between soil pH and *H. glycines* population densities and subsequent effect on yield. Experiments were conducted in Wisconsin from 1997 to 2000 and in Iowa from 1996 to 1998. Results were consistent among the experiments and showed a positive correlation between soil pH and *H. glycines* population densities and a negative correlation between yield and both soil pH and *H. glycines* population densities in both states. In the Wisconsin experiment, yield of both *H. glycines*-resistant and *H. glycines*-susceptible cultivars decreased as pH increased, but the decrease was less with *H. glycines*-resistant cultivars. Overall, results indicate that *H. glycines* population densities and the impact of nematode population densities on soybean yield are related to soil pH; however, the mechanism of these interactions is unknown.

P. Pedersen and A. Mallarino, Dep. of Agronomy, Iowa State Univ., Ames, IA 50011; G.L. Tylka, Dep. of Plant Pathology, Iowa State Univ., Ames, IA 50011; A.E. MacGuidwin, N.C. Koval, and C.R. Grau, Dep. of Plant Pathology, Univ. of Wisconsin, Madison, WI 53706. Current address for P. Pedersen, Syngenta Crop Protection, 2415 Clayton Drive, Ames, IA 50010. Received 7 Aug. 2009. \*Corresponding author (palle.pedersen@syngenta.com).

**Abbreviations:** Pf, final *H. glycines* egg population densities; Pi, initial *H. glycines* egg population densities.

SOIL pH above 7.4 is considered high for a commercial soybean [*Glycine max* (L.) Merr.] field (Sawyer et al., 2002). In general, a soil pH above 6.3 is considered ideal for leguminous crops (Schulte and Walsh, 1995). Soil pH is important for optimal plant growth because it affects the availability of essential nutrients (Schulte and Walsh, 1995) and influences activity of *Bradyrhizobium japonicum*, responsible for nitrogen fixation, and numerous other microorganisms. Soybean yield did not differ in soil pH from 5.4 to 7.8 in fields not infested with *H. glycines* in Iowa (Pedersen, 2005).

Associations of soilborne plant pathogens with soil pH and the subsequent effect of pH on disease severity have been reported for many crops. Disease severity can be reduced by acidification of soil in many pathosystems, including scab of potato (*Solanum tuberosum* L.), caused by *Streptomyces scabies* (Martin, 1920), take-all of wheat (*Triticum aestivum* L.), caused by *Gaeumannomyces graminis* var. *tritici* (Trolldenier, 1981), and Phytophthora root rot on many crops (Schmitthenner and Canaday, 1983). In soybean, Sanogo and Yang (2001) found that development of sudden death syndrome, caused by *Fusarium virguliforme* O'Donnell & Aoki

Published in Crop Sci. 50:1458–1464 (2010).

doi: 10.2135/cropsci2009.08.0432

Published online 20 Apr. 2010.

© Crop Science Society of America | 5585 Guilford Rd., Madison, WI 53711 USA

All rights reserved. No part of this periodical may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage and retrieval system, without permission in writing from the publisher. Permission for printing and for reprinting the material contained herein has been obtained by the publisher.

[synonym *F. solani* (Mart.) Sacc. f. sp. *glycines*] (Akoi et al., 2002) was greater at soil pH of 7.7 than a soil pH of 5.5. Brown stem rot, caused by *Phialophora gregata*, is most severe at soil pH below 6.5, and as soil pH approaches 7.0, both foliar symptoms and internal stem browning decrease (Kurtzweil and Grau, 2001).

Most plant-parasitic nematodes are soilborne, and at least part of their life cycle occurs in the soil. Consequently, edaphic factors may directly affect their distribution and population dynamics. Several researchers have investigated the relationship of soil pH and plant-parasitic nematodes. Burns (1971) reported greater colonization of soybean roots by the root-lesion nematode *Pratylenchus allenii* when plants were grown at pH 6.0 and 8.0 than at pH 4.0. Norton et al. (1971) detected significant negative correlations between soil pH in a soybean field and population densities of the lance nematode, *Hoplolaimus galeatus*, the dagger nematode, *Xiphinema americanum*, and the stunt nematode, *Tylenchorhynchus nudus*, but a significant positive correlation between population densities of the spiral nematode, *Helicotylenchus pseudorobustus*, and soil pH also was reported (Norton et al., 1971).

Several life stages of *Heterodera* spp., the lemon-shaped cyst nematodes, occur in the soil and may be directly affected by soil pH. These life stages include egg-mass and encysted eggs, second-stage juveniles, and adult males. Females develop from second-stage juveniles embedded within root tissue and eventually break through the root tissue as they fully develop and become exposed to the soil environment on the surface of the root. Nematodes also may be indirectly affected by soil factors through the host plant (Burns, 1971).

Duggan (1963) was the first to report a relationship between soil pH and population densities of *Heterodera* cyst nematodes. In a survey conducted in Scotland, cyst population densities of *H. avenae* were found to be positively correlated with soil pH (Duggan, 1963). In 1993, Francl reported that soil pH and magnesium levels were significantly and positively related to *H. glycines* soil population densities (Francl, 1993). In a greenhouse experiment, Anand et al. (1995) found that greater numbers of *H. glycines* females formed on roots of a susceptible and four resistant soybean cultivars at pH 6.5 and 7.5 than at 5.5.

The best strategies to manage *H. glycines* include growing *H. glycines*-resistant soybean cultivars in rotation with nonhost crops (Donald et al., 2006). Unfortunately, above-ground symptoms of *H. glycines* are not always obvious (Wang et al., 2003), and many growers first start managing *H. glycines* when the population densities are high. No yield drag exists between *H. glycines*-resistant and *H. glycines*-susceptible cultivars today (De Bruin and Pedersen, 2008a,b), and the yield advantage for planting *H. glycines*-resistant cultivars in *H. glycines*-infested fields is, on average, 10% (Donald et al., 2006).

Spatial variability of plant-parasitic nematodes may reflect, to some extent, variability in the soil environment (Noe and Barker, 1985). However, results on the relationships of soil properties and plant-parasitic nematodes are sometimes conflicting and may be field specific. In the Des Moines loess soil region in north central Iowa and south central Minnesota, soils are calcareous, with moderate to high soil pH (Steinwand and Fenton, 1995). Rogovska et al. (2009) found in an on-farm study in Iowa that soybean yield decreased as soil pH, CaCO<sub>3</sub> equivalent (CCE), alkalinity stress index (combines pH and CCE), and *H. glycines* population densities increased. In Wisconsin, soybeans are produced in a wide range of cropping systems and soil pH levels. Soil pH may account for a portion of the variability in detection and densities of *H. glycines* in Wisconsin.

Our hypothesis is that soil pH and *H. glycines* population densities are related and that the yield advantage of growing *H. glycines*-resistant cultivars rather than *H. glycines*-susceptible cultivars increases as soil pH increases. The objectives of our study were (i) to validate the relationship between soil pH and *H. glycines* population densities, (ii) to assess the relationship between soil pH and *H. glycines* population densities and subsequent effect on soybean yield, and (iii) to evaluate the yield advantage of *H. glycines*-resistant cultivars across a soil pH gradient. A preliminary report of a portion of this work has been previously published (Tylka et al., 1998).

## MATERIALS AND METHODS

### Wisconsin High-Intensity, Small-Plot Research Experiments (1997–2000)

A field study was conducted during 4 yr (1997 to 2000) at East Troy, WI, in a field with a pH gradient from 5.4 to 8.4 across the field (Table 1). *Heterodera glycines* was first identified in the field in 1993, and corn (*Zea mays* L.) was grown from 1994 to 1996. Soybean cultivars susceptible to *H. glycines* used in this study were Asgrow AG2701 and Novartis NK 24-92 in 1997; Asgrow AG2101 and Novartis NK 24-92 in 1998; Asgrow AG2101, Asgrow AG2553, Trelay 248, and Spansoy 228 in 1999; and Dairyland 241 in 2000. Cultivars resistant to *H. glycines* used in this study were Asgrow AG2901 and Pioneer 92B91 in 1997; Asgrow AG2201 and Pioneer 9234 in 1998; Asgrow AG2201, Mark98CN28, DeKalb CX235, and Pioneer 9234 in 1999; and Asgrow AG2201 in 2000. Each plot consisted of eight 7.6-m-long rows spaced 76-cm apart. Seeds were planted 4-cm deep at a rate of 385,000 seeds ha<sup>-1</sup>. Plots always followed corn, with the physical placement of the plots rotated in two different areas adjacent to each other.

The plots received one of three weed-management treatments: (i) a no-herbicide, mechanically weeded control, (ii) preemergence-applied pendimethalin [N-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzamine] at 1.39 kg a.i. ha<sup>-1</sup>, postemergence-applied acifluorfen at 0.42 kg a.i. ha<sup>-1</sup> + 1% (v/v) crop oil concentrate (COC), and (iii) postemergence-applied glyphosate [N-(phosphonomethyl)glycine] at 1.12 kg a.i. ha<sup>-1</sup>.

The preemergence herbicides were applied after planting but before soybean emergence, and postemergence herbicides were applied at growth stage V4 (Fehr and Caviness, 1977). Glyphosate was applied to the glyphosate-tolerant cultivars only, which were Asgrow AG2701 and Asgrow AG2901 in 1997, Asgrow AG2101 and Asgrow AG2201 in 1998 and 1999, and Dairyland 241 and Asgrow AG2201 in 2000.

*Heterodera glycines* egg population densities were determined in each plot at planting (initial population density, or Pi) and at harvest (final population density, or Pf). Eight soil cores, 2.5-cm diam. × 20-cm deep, were collected from the center two rows per plot in an arbitrary zigzag pattern, and cores from the same plot were combined. Cysts were extracted from a 100 cm<sup>3</sup> subsample of each sample by gravity sieving with a 710-μm-pore sieve nested over a 180-μm-pore sieve and counted. Eggs were extracted from the cysts using a stainless steel pestle and were recovered on a 25-μm-pore sieve, then stained with acid fuchsin (Niblack et al., 1993) and counted.

In addition to determining *H. glycines* egg population densities in each plot, soil samples also were taken before planting and analyzed for soil pH, organic matter, and macronutrients at the University of Wisconsin Soil and Plant Analysis Laboratory (Madison, WI; Table 1). Additional data collected during all years included seed yield and seed moisture. An Almaco plot combine (Almaco, Nevada, IA) was used to harvest the center two rows from each plot. Seed yields were adjusted to moisture content of 130 g kg<sup>-1</sup>.

All data were subjected to an analysis of variance using the PROC MIXED procedure of SAS (SAS Institute, 2003). Since some herbicides could only be applied to certain cultivars, each herbicide-cultivar combination was considered a treatment. The experiment was a randomized complete block design with four replications, where treatments were randomized each year across the pH gradient. Homogeneity of variance for cultivars was tested by Bartlett's  $\chi^2$  test (Steele and Torrie, 1980) to group cultivars into two classes, either *H. glycines* susceptible or *H. glycines* resistant, and analyses were done to compare the two classes of soybean cultivars. Years were analyzed separately because the cultivars used each year varied. Except for replications, other variables were treated as fixed effects in determining the expected mean square and appropriate *F* tests in the analysis of variance. All *H. glycines* data were transformed to log<sub>10</sub> (*x* + 1) values before statistical analysis. Regressions between soil pH and seed yield and initial and final *H. glycines* egg population densities were done using PROC REG of SAS (SAS Institute, 2003). Data were analyzed by correlation and path coefficient analysis because measured variables were not independent. Simple correlation coefficients were computed using PROC CORR of SAS (SAS Institute, 2003), and path analysis was conducted using the PROC CALIS function of SAS (SAS Institute, 2003).

## Iowa Large-Scale, Grid Sampling Experiments (1996–1998)

Experiments were conducted in areas located in two soybean production fields near Perry, IA. Fields, naturally infested with *H. glycines*, were cropped to alternating years of corn and *H. glycines*-susceptible soybeans in the years before the initiation of the experiment. The fields were characterized for factors germane to the study (Table 1).

**Table 1. Field characteristics for the various experiments conducted in Wisconsin and Iowa from 1996 to 2000.**

	East Troy, WI <sup>†</sup>	Perry, IA
Latitude	42°6' N	42°0' N
Soil series <sup>‡</sup>	Matherton silt loam	Canisteo clay loam
Soil family	Fine loamy, mixed, mesic Typic Endoaqualls	Fine-loamy, mixed, mesic Typic Haplaquolls
Range of soil fertility <sup>§</sup>		
pH	5.4–8.4	5.6–7.8
P, mg kg <sup>-1</sup>	1–125	7–72
K, mg kg <sup>-1</sup>	65–350	60–190
Organic matter, g kg <sup>-1</sup>	15–115	29–127

<sup>†</sup>Experiments at East Troy, WI, were conducted from 1997 to 2000, and the experiments at Perry, IA, were conducted from 1996 to 1998.

<sup>‡</sup>The most common soil type across the experiment areas.

<sup>§</sup>Ranges across years.

The study area in each field was comprised as a contiguous 20-ha block that was partitioned into 100 0.2-ha square grid cells. Comanche IV, an *H. glycines*-susceptible soybean cultivar (Merschman Seeds, West Point, IA), was grown in 1996 and 1998 in one field, and the *H. glycines*-susceptible soybean cultivar Apache V (Merschman Seeds, West Point, IA) was grown in 1997 in the other field. Soil samples were collected from each grid cell in the spring and fall of 1996, 1997, and 1998 within a week of planting and harvesting. Soil samples consisted of 10 2.5-cm-diam. × 20-cm deep soil cores collected from a 6-m-diam. circular area centered on a randomly selected location within each 0.2-ha grid cell. The soil cores from each sample site were mixed and combined. *Heterodera glycines* egg population densities were determined from a 100 cm<sup>3</sup> subsample of each soil sample, and the remaining soil was used for soil pH analyses. The *H. glycines* cysts were extracted from the soil by elutriation (Byrd et al., 1976) and were collected on a 250-μm-pore sieve. Eggs were extracted from cysts using a motorized pestle and were stained in acid fuchsin (Niblack et al., 1993) and counted. The remaining soil from each sample was sent to Minnesota Valley Testing Laboratories (Nevada, IA) for analyses of soil pH, organic matter, and macronutrients.

Yield was collected from the yield monitor of a commercial scale combine (Case IH 2188, Racine, WI) and adjusted to 130 g kg<sup>-1</sup> moisture level. Data was analyzed using methods similar to the analysis described above for the study at East Troy, WI.

## RESULTS

### Wisconsin High-Intensity, Small-Plot Research Experiments (1997–2000)

*Heterodera glycines* was distributed throughout the experimental site, but population densities varied across the pH gradient in each field. Except for one plot with pH of 5.4 in 1999, *H. glycines* was found in all plots, with the greatest Pi being 28,900 eggs 100<sup>-1</sup> cm<sup>-3</sup> soil. The greatest *H. glycines* Pf was 49,600 eggs 100<sup>-1</sup> cm<sup>-3</sup> soil. Differences in yield were observed among years, and overall average soybean yields were 2985, 4449, 2718, and 2630 kg ha<sup>-1</sup> in 1997, 1998, 1999, and 2000, respectively. There were



no significant differences in relationships among soil pH values, *H. glycines* population densities, and soybean yields among the weed management treatments (data not shown).

The data were consistent among years (Table 2). For data combined for all cultivars, pH and *H. glycines* population densities (Pi and Pf) were positively correlated ( $P < 0.01$ ). Also, yield was negatively correlated ( $P < 0.01$ ) with both pH and *H. glycines* population densities (Pi and Pf). Except for 2000, Pf values were positively correlated with Pi.

The regression analysis of yield vs. soil pH for *H. glycines*-resistant and *H. glycines*-susceptible cultivars was significant for all 4 yr (Table 3). The linear regression model gave a better fit than the quadratic and log-linear models on the basis of model significance and coefficient of determination ( $R^2$ ) values in PROC REG of SAS. Strong linear relationships ( $P < 0.001$ ) were observed for both resistant and susceptible cultivars during all years (Table 3). The only outlier was during 1999 for the resistant cultivars, where a weaker, but still significant ( $P = 0.03$ ), effect was observed. Coefficient of determination values for susceptible cultivars ranged from 0.64 to 0.77, whereas the coefficient of determination values for resistant cultivars were much lower, ranging from 0.08 to 0.40.

Yield differences between *H. glycines*-resistant and *H. glycines*-susceptible cultivars increased as pH increased (Table 3). Yield of both *H. glycines*-resistant and *H. glycines*-susceptible cultivars decreased as pH increased, but the decrease was less with *H. glycines*-resistant cultivars.

Simple linear correlation coefficients ranged from  $-0.58$  to  $-0.72$  for soil pH and seed yield (Table 2). Path coefficient analysis showed that partitioning of the effects

indicated a direct effect of only  $-0.01$  to  $-0.43$ , except in 1997, when a positive effect of 0.38 was observed for the direct effect (Table 4).

## Iowa Large-Scale, Grid-Sampling Experiments (1996–1998)

*Heterodera glycines* was found in 92% of the soil samples both during the spring and fall soil sampling. Population densities ranged from 0 to 31,400 eggs  $100^{-1} \text{ cm}^{-3}$  soil for Pi and from 0 to 49,800 eggs  $100^{-1} \text{ cm}^{-3}$  soil for Pf. Overall, average soybean yields were 2957, 2313, and 3898 kg  $\text{ha}^{-1}$  in 1996, 1997, and 1998, respectively.

Soil pH was consistently inversely correlated ( $P < 0.01$ ) with yield; correlation coefficients ranged from  $-0.61$  to  $-0.79$  (Table 5). Soil pH was positively correlated ( $P < 0.01$ ) with Pi in 1997 and 1998 and positively correlated ( $P < 0.01$ ) with Pf in 1996 and 1997. Yield was inversely correlated ( $P < 0.01$ ) with Pf, and correlation coefficients ranged from  $-0.39$  and  $-0.57$ . In 1997 and 1998, negative correlations ( $P < 0.01$ ) of 0.47 and 0.60 were observed between seed yield and Pi.

The regression analysis of yield vs. soil pH was significant for all 3 yr (Table 6). Strong linear relationships ( $P < 0.001$ ) were observed, with the linear regression model again giving a better fit than the quadratic and log-linear models. Coefficient of determination values ranged from 0.38 to 0.63. Simple linear correlation coefficients ranged from  $-0.61$  to  $-0.79$  for pH on yield (Table 2). Path coefficient analysis partitioning of the effects indicated a direct effect of only  $-0.16$  to  $-0.39$  (Table 4).

## DISCUSSION

The relationship of *H. glycines* with soil pH was studied in experiments conducted in three naturally infested fields in Wisconsin and Iowa. The experimental approaches used varied in the studies from small-plot research with intensive sampling to large-plot and low-intensity grid sampling. Despite the use of multiple types and scales of experiments, multiple soil sampling approaches, numerous years of research, different locations and soil types, and multiple soybean cultivars, the positive correlation between *H. glycines* and soil pH was consistently strong and highly significant.

The relationship between *H. glycines* and soil pH was first reported by Francl (1993), and our data are consistent with the observation reported in that paper. However, our data are unique in that they show that the relationship occurs over a broad range of soil conditions and geographic regions and that the relationship also affects seed yield. Our data also showed a significant yield advantage of using *H. glycines*-resistant cultivars in a high vs. low soil pH. We were able to document the relationship between *H. glycines* population densities and soil pH over a larger range of soil pH (5.4–8.4) and soil types than the previous

**Table 2. Simple linear correlation coefficients ( $r$ ) between seed yield, soil pH, initial (Pi), and final *Heterodera glycines* egg (Pf) population densities across cultivars near East Troy, WI, 1997 to 2000.**

	pH	Pi	Pf
		1997	
Yield	$-0.61^{**}$	$-0.55^{**}$	$-0.70^{**}$
pH	–	0.82**	0.39**
Pi	–	–	0.46**
		1998	
Yield	$-0.71^{**}$	$-0.55^{**}$	$-0.50^{**}$
pH	–	0.76**	0.39**
Pi	–	–	0.25*
		1999	
Yield	$-0.58^{**}$	$-0.29^{**}$	$-0.60^{**}$
pH	–	0.31**	0.51**
Pi	–	–	0.18*
		2000	
Yield	$-0.72^{**}$	$-0.42^{**}$	$-0.30^{**}$
pH	–	0.47**	0.30**
Pi	–	–	0.03

\*Significant at the 0.05 probability level.

\*\*Significant at the 0.01 probability level.

**Table 3. Regression analysis and predicted soybean seed yield for *Heterodera glycines*–resistant and *H. glycines*–susceptible cultivars grown in soil with varying soil pH in a field near East Troy, WI, 1997 to 2000.**

Year	Cultivar	Linear regression†	Model significance	R <sup>2‡</sup>	Predicted yield of a soil pH of						
					5.0	5.5	6.0	6.5	7.0	7.5	8.0
kg ha <sup>-1</sup>											
1997	Resistant	Y = −191.3X + 4633.9	P < 0.001	0.31	3677	3582	3486	3390	3295	3199	3104
	Susceptible	Y = −600.9X + 6674.7	P < 0.001	0.77	3670	3370	3069	2769	2468	2168	1868
	Yield advantage using a <i>H. glycines</i> –resistant cultivar				7	212	417	621	827	1031	1236
1998	Resistant	Y = −266.5X + 6451.0	P < 0.001	0.40	5119	4985	4852	4719	4586	4452	4319
	Susceptible	Y = −579.4X + 8367.6	P < 0.001	0.74	5471	5181	4783	4602	4312	4022	3732
	Yield advantage using a <i>H. glycines</i> –resistant cultivar				−352	−196	69	117	274	430	587
1999	Resistant	Y = −128.5X + 3720.7	0.03	0.08	3078	3014	2950	2885	2821	2757	2693
	Susceptible	Y = −654.3X + 6897.4	P < 0.001	0.67	3626	3299	2972	2644	2317	1990	1663
	Yield advantage using a <i>H. glycyines</i> –resistant cultivar				−548	−285	−22	241	504	767	1030
2000	Resistant	Y = −413.8X + 5654.3	P < 0.001	0.36	3585	3378	3172	2965	2758	2551	2344
	Susceptible	Y = −562.6X + 6588.4	P < 0.001	0.64	3775	3494	3213	2932	2650	2369	2088
	Yield advantage using a <i>H. glycines</i> –resistant cultivar				−190	−116	−41	33	108	182	256

†Y, soybean yield in kg ha⁻¹; X, soil pH.

‡R², coefficient of determination.

**Table 4. Path analysis of direct and indirect effects of relationships between soil pH, *Heterodera glycines* initial (Pi) and final (Pf) population densities, and soybean seed yield at East Troy, WI, 1997 to 2000 and at Perry, IA, 1996 to 1998.**

	East Troy, WI				Perry, IA		
	1997	1998	1999	2000	1996	1997	1998
Soil pH vs. Yield†	–0.61	–0.71	–0.58	–0.72	–0.61	–0.79	–0.74
Direct effect	0.38	–0.01	–0.16	–0.43	–0.39	–0.16	–0.28
Indirect effect							
Indirect effect via Pf	–0.27	–0.20	–0.30	–0.09	–0.23	–0.28	–0.01
Indirect effect via Pi	–0.45	–0.41	–0.09	–0.20	0.01	–0.24	–0.46
Indirect effect via Pi and Pf	–0.26	–0.10	–0.03	0.00	0.00	–0.11	0.00

†Simple correlation coefficients from Table 3 and 5.

report by Francl, who studied one soil type and a pH range from 5.0 to 6.4 (Francl, 1993).

The nature or basis of the relationship between *H. glycines* and soil pH is still an unknown. Obviously, soil pH cannot affect whether the nematode is introduced into the field, but it likely can affect eventual establishment of *H. glycines* infestations. We know that soil pH in the range of 5.4 to 7.8 does not directly influence yield in fields not infested with *H. glycines* in Iowa (Pedersen, 2005), but soil pH will influence nutrient availability (Sawyer et al., 2002; Schulte and Walsh, 1995). We hypothesize that soil pH may have an indirect effect on *H. glycines* biology and/or behavior or the soil pH may affect the suitability or susceptibility of the soybean plant to serve as a host to the obligately parasitic nematode. Another possibility is that soil pH may affect some other aspects of the soil environment that affect the biology and/or behavior of the nematode.

Path coefficient analysis was used to partition effect of each measured variable (pH, Pi, and Pf) on yield, because measured variables were not independent. Correlation and path analysis allows for the partitioning of the various effects of each measured variable into direct effects on yield and indirect effects through other variables (pH, Pi, and Pf), which in turn affect yield. Differences exist

**Table 5. Simple correlation coefficients (r) between soybean seed yield, soil pH, and *Heterodera glycines* initial (Pi) and final (Pf) egg population densities near Perry, IA, 1996 to 1998.**

	pH	Pi	Pf
		1996	
Yield	–0.61**	0.15	–0.39**
pH	–	0.05	0.60**
Pi	–	–	0.10
1997			
Yield	–0.79**	–0.47**	–0.57**
pH	–	0.57**	0.49**
Pi	–	–	0.43
1998			
Yield	–0.74**	–0.60**	–0.39**
pH	–	0.79**	–0.06
Pi	–	–	–0.07

\*\*Significant at the 0.01 probability level.

for the seven environments, but overall the indirect effect of pH on yield via *H. glycines* Pi, Pf, and Pf through Pi accounts for most of the effects represented by the simple correlation coefficient. This indicated that the greatest impact of pH on yield is through its effect on *H. glycines* Pi and Pf.

**Table 6. Regression equations and predicted soybean seed yields for selected soil pH near Perry, IA, 1996 to 1998.**

Year	Linear regression†	Model significance	R <sup>2‡</sup>	Predicted yield of a soil pH of						
				5.0	5.5	6.0	6.5	7.0	7.5	8.0
1996	Y = −619.6X + 7268.9	P < 0.001	0.38	4171	3861	3551	3242	2932	2622	2312
1997	Y = −648.6X + 6582.5	P < 0.001	0.63	3340	3015	2691	2367	2042	1718	1394
1998	Y = −469.5X + 7048.8	P < 0.001	0.55	4701	4467	4232	3997	3762	3528	3293

†Y, soybean yield in kg ha⁻¹; X, soil pH.

‡R², coefficient of determination.

Typically, low pH has been considered a more serious constraint on soybean productivity than high pH; for optimal soybean growth it is recommended to lime a field if the soil pH is below 6.5 (Sawyer et al., 2002). So the *H. glycines* and soil pH relationship we have detected is somewhat counterintuitive as it relates to soybean growth. *Heterodera glycines* is an obligate parasite and is dependent on the plant for the nutrition required to complete its life cycle. One would not expect high population densities of an obligate parasite to develop on a host that is not growing optimally. Yet we detected the highest *H. glycines* population densities in plots with pH values well above those considered optimum for soybean.

*Heterodera glycines*-resistant cultivars are an important management tactic to use in all fields infested with the nematode. However, soil pH may influence the relative performance of *H. glycines*-resistant and *H. glycines*-susceptible cultivars. Recent research conducted in Iowa documented that no yield drag exists between *H. glycines*-resistant and *H. glycines*-susceptible cultivars (De Bruin and Pedersen, 2008a,b). Our data illustrate that the greatest yield benefit of *H. glycines*-resistant cultivars is achieved in high pH soil environments.

The high coefficients of determination values obtained for the regressions of nematode population densities and yields for *H. glycines*-susceptible cultivars in the experiments in Wisconsin indicate that the *H. glycines*-susceptible cultivars used were consistently low yielding and the variability among them was small. Conversely, the low coefficient of determination values for regressions of nematode population densities and yields for the *H. glycines*-resistant cultivars in the Wisconsin experiments indicate that the variability among *H. glycines*-resistant cultivars was large, that not all *H. glycines*-resistant cultivars were equal for resistance, and possibly that the *H. glycines* population or HG (*Heterodera glycines*; Niblack et al., 2002) type in the field had broad ability to reproduce on the resistant soybean cultivars grown in the experiment.

Yield of both *H. glycines*-susceptible and resistant cultivars declined as soil pH increased in the experiments conducted in Wisconsin; however, the magnitude of yield difference increased between each group of cultivars as soil pH increased. The difference in yield between *H. glycines*-susceptible and resistant cultivars was most likely due to control of the nematode rather than resistant

cultivars being tolerant of yield-limiting effects associated with high soil pH. However, Chen et al. (2007) reported that symptoms of iron-deficiency chlorosis were greater in soybean cultivars susceptible to *H. glycines* than those resistant to the nematode when grown in a field infected with *H. glycines*, so infection by the nematode may somehow increase the symptoms of iron-deficiency chlorosis. Iron-deficiency chlorosis was not observed at any location during this study.

## CONCLUSIONS

Our data indicate that soil pH is a useful guide to researchers, agronomists, and farmers attempting to account for natural variability of *H. glycines* population densities without prior knowledge of the nematode's distribution in a field. On the basis of our results, agronomists and farmers would be well served to assay areas of high pH in fields to determine the presence or absence of *H. glycines*. Soybean and nematology researchers should be cognizant that *H. glycines* population densities may be greater in high pH soil relative to soil with neutral or acidic pH. And soybean breeders developing resistant cultivars for management of *H. glycines* should be aware that those resistant cultivars should also possess good tolerance to iron-deficiency chlorosis if intended to be used for *H. glycines* management in areas of the United States where high soil pH is prevalent. Soybean breeders should take soil pH into account when establishing *H. glycines* nurseries for their breeding program. Additional research is needed to determine the mechanism of the *H. glycines*-pH relationship.

## References

- Akoi, T., K. O'Donnell, and M.M. Scandiani. 2002. Sudden death syndrome of soybean in South America is caused by four species of *Fusarium*: *Fusarium brasiliense* sp. nov., *F. cuneirostrum* sp. nov., *F. tucumaniae*, and *F. virguliforme*. *Mycoscience* 46:162–183.
- Anand, S.C., S.R. Koenning, and S.B. Sharma. 1995. Effect of temporal deployment of different sources of resistance to soybean cyst nematode. *J. Prod. Agric.* 8:119–123.
- Burns, N.C. 1971. Soil pH effects on nematode populations associated with soybeans. *J. Nematol.* 3:238–245.
- Byrd, D.W., Jr., K.R. Barker, H. Ferris, C.J. Nusbaum, W.E. Griffin, R.H. Small, and C.A. Stone. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. *J. Nematol.* 8:206–212.
- Chen, S., J.E. Kurle, S.R. Stetina, D.R. Miller, L.D. Klossner, G.A. Nelson, and N.C. Hansen. 2007. Interactions between

- iron-deficiency chlorosis and soybean cyst nematode in Minnesota soybean fields. *Plant Soil* 299:131–139.
- De Bruin, J., and P. Pedersen. 2008a. Response of old and new soybean cultivars to *Heterodera glycines* Ichinohe. *Agron. J.* 100:1347–1353.
- De Bruin, J., and P. Pedersen. 2008b. Yield improvement and stability for soybean cultivars with resistance to *Heterodera glycines* Ichinohe. *Agron. J.* 100:1354–1359.
- Donald, P.A., P.E. Pierson, S.K. St. Martin, P.R. Sellers, G.R. Noel, A.E. MacGuidwin, J. Faghihi, V.R. Ferris, C.R. Grau, D.J. Jardine, H. Melakeberhan, T.L. Niblack, W.C. Stienstra, G.L. Tylka, T.A. Wheeler, and D.S. Wysong. 2006. Assessing *Heterodera glycines*-resistant and susceptible cultivar yield response. *J. Nematol.* 38:76–82.
- Duggan, J.J. 1963. Relationship between intensity of cereal root eelworm (*Heterodera avenae* Wollenweber 1924) infestation and pH value of soil. *Ir. J. Agric. Res.* 2:105–110.
- Fehr, W.R., and C.E. Caviness. 1977. Stages of soybean development. Spec. Rep. 80. Iowa Agric. Home Econ. Exp. Stn., Iowa State Univ., Ames, IA.
- Francl, L.J. 1993. Multivariate analysis of selected edaphic factors and their relationship to *Heterodera glycines* population density. *J. Nematol.* 25:270–276.
- Kurtzweil, N.C., and C.R. Grau. 2001. Relationship of soil pH and brown stem rot of soybean. (Abstr.). *Phytopathology* 91:S178.
- Martin, W.H. 1920. The relation of sulphur to soil acidity and to the control of potato scab. *Soil Sci.* 9:393–409.
- Niblack, T.L., R.D. Heinz, G.S. Smith, and P.A. Donald. 1993. Distribution, density, and diversity of *Heterodera glycines* in Missouri. *Suppl. J. Nematol.* 25:880–886.
- Niblack, T.L., R.D. Riggs, P.R. Arelli, G.R. Noel, C.H. Opperman, J.H. Orf, D.P. Schmitt, J.G. Shannon, and G.L. Tylka. 2002. A new classification scheme for genetically diverse populations of *Heterodera glycines*. *J. Nematol.* 34:279–288.
- Noe, J.P., and K.R. Barker. 1985. Relation of within-field spatial of plant-parasitic nematode population densities and edaphic factors. *Phytopathology* 75:247–252.
- Norton, D.C., L.R. Frederick, P.E. Ponchillia, and J.W. Nyhan. 1971. Correlations of nematodes and soil properties in soybean fields. *J. Nematol.* 3:154–163.
- Pedersen, P. 2005. Effects of soil pH on soybean grain yield and composition. In *Annual Meetings Abstract* [CD-ROM computer file]. ASA Annual Meetings, Salt Lake City, UT. 6–10 Nov. 2005. ASA, Madison, WI.
- Rogovska, N.P., A.M. Blackmer, and G.L. Tylka. 2009. Soybean yield and soybean cyst nematode densities related to soil pH, soil carbonate concentrations and alkalinity stress index. *Agron. J.* 101:1019–1026.
- Sanogo, S., and X.B. Yang. 2001. Relation of sand content, pH, and potassium and phosphorus nutrition to the development of sudden death syndrome in soybean. *Can. J. Plant Pathol.* 23:174–180.
- SAS Institute. 2003. The SAS system for Microsoft Windows. Release 9.1. The SAS Institute Inc., Cary, NC.
- Sawyer, J.E., A.P. Mallarino, R. Killorn, and S.K. Barnhart. 2002. A general guide for crop nutrient and limestone recommendations in Iowa. PM 1688. Iowa State Univ. Ext. Publication. Iowa State Univ., Ames, Iowa.
- Schmitthenner, A.F., and C.H. Canaday. 1983. Role of chemical factors in the development of *Phytophthora* diseases. p. 189–196. In D.C. Erwin et al. (ed.) *Phytophthora. Its biology, taxonomy, ecology, and pathology*. American Phytopathological Society, St. Paul, MN.
- Schulte, E.E., and L.M. Walsh. 1995. Management of Wisconsin soils. 4th ed. Univ. of Wisconsin-Extension. Cooperative extension publication A3588. Madison, WI.
- Steele, R.G.D., and J.G. Torrie. 1980. Principles and procedures of statistics: A biometrical approach. 2nd ed. McGraw-Hill, New York.
- Steinwand, A.L., and T.E. Fenton. 1995. Landscape evolution and shallow groundwater hydrology of a till landscape in central Iowa. *Soil Sci. Soc. Am. J.* 59:1370–1377.
- Trolldenier, G. 1981. Influence of soil moisture, soil acidity, and nitrogen source on take-all of wheat. *J. Phytopathol.* 102:163–177.
- Tylka, G.L., C. Sanogo, and S.K. Souhrada. 1998. Relationships among *Heterodera glycines* population densities, soybean yields, and soil pH. (Abstr.). *J. Nematol.* 30:519–520.
- Wang, J., T.L. Niblack, J.N. Tremaine, W.J. Wiebold, G.L. Tylka, C.C. Marett, G.R. Noel, O. Myers, and M.E. Schmidt. 2003. The soybean cyst nematode reduces soybean yield without causing obvious symptoms. *Plant Dis.* 87:623–628.